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DEVELOPMENTAL MORPHOLOGY OF THE CARYOPSIS IN MAIZE[1]

By L. F. RANDOLPH[2]

Cytologist, Division of Cereal Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture, and *associate in research (cytology), New York (Cornell) Agricultural Experiment Station*

INTRODUCTION

In recent years the maize plant has been the subject of extensive genetical, cytological, and physiological investigations. Many of these investigations have been concerned primarily with the kernel or caryopsis, while others have required a prerequisite knowledge of the developmental morphology of the plant, especially in the early stages. The object of the present study was to trace the developmental morphology of the kernel in an effort to determine not only the manner of development but also the order and rate of development of the various parts. Such a study of the normal development of the caryopsis in ordinary varieties would serve as a starting point for investigations of the various kernel types in numerous other varieties and abnormal genetical strains of maize. It was hoped that the investigation might clarify certain questions concerning the comparative morphology of maize and related grasses and also provide a more adequate basis for researches on maize in allied fields of investigation.

REVIEW OF LITERATURE

The developmental morphology of the caryopsis in maize (*Zea mays* L.) has been studied by numerous investigators, beginning with the classic researches of the early morphologists published during the middle of the last century. References to *Zea* are to be found in the important works of Schleiden (*37*),[3] Hofmeister (*21*), Schacht (*36*), and Van Tieghem (*46*). As early as 1872 the highly specialized nature of the maize embryo was fully recognized by Van Tieghem, who considered it a type distinct from that of other grasses, a distinction which has since come to be generally recognized. Prior to 1900 the general morphology of the caryopsis had been described and compared with that of related forms by True (*47*), Kennedy (*23*), and others. The essential features of double fertilization in maize were clearly

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[2] The writer wishes to acknowledge the very helpful assistance of Fannie Rane Randolph in the examination and interpretation of the material and in the preparation of many of the illustrations.

[3] Reference is made by number (italic) to Literature Cited, p. 913.

outlined by Guignard (*16*) in 1901, 3 years after Nawaschin (*31*) discovered the process in *Lilium*. More recently Miller (*30*), Weatherwax (*51*), and Rhoades [4] have given accounts of fertilization in maize.

The early stages in embryogeny and endosperm development and the structure of the embryo and endosperm at maturity have been studied by Weatherwax and a number of other workers, but relatively little attention has been devoted to the important intermediate stages. True (*47*), Guérin (*15*), Poindexter (*33*), Weatherwax (*52*), Randolph (*34*), and Haddad (*19*) traced the histological changes which take place during the transformation of the ovary wall into the pericarp of the mature grain. The presence at maturity of a testa consisting of integument tissue was described by Weatherwax, and True also indicated that both integument and nucellar remnants were present in the fully developed kernel. However, Guérin, Poindexter, and F. R. Randolph found little or no trace of either integument or nucellar tissue in the ripe grain.

The existence of a specialized semipermeable "seed-coat membrane" in the maize caryopsis was suggested by the physiological researches of Shull and Shull (*40*), Beeskow,[5] Orton (*32*), and Tharp.[6] Beeskow attributed this functional semipermeability in maize to several layers of chiefly disorganized cells between the pericarp and the endosperm. In the related grasses *Sorghum*, *Hordeum*, *Triticum*, and *Poa* the presence of a definite suberized semipermeable membrane has been demonstrated both physiologically and morphologically by Brown (*5*, *6*), Harrington and Crocker (*20*), Andersen (*1*), Gurewitsch (*17*), and Krauss (*24*). In the present study a similar well-defined suberized layer was observed in maize, and its developmental history was carefully traced.

MATERIAL AND METHODS

The material for these studies was obtained from commercial varieties of maize grown under ordinary field conditions in the experimental garden of the Department of Plant Breeding at Ithaca, N. Y. The dent variety Pride of Michigan furnished most of the material, but other varieties of dent corn as well as sugary and flint types were examined. However, no significant morphological differences were noted among the different types other than variations which might readily be attributed to differences in the size, shape, or degree of maturity of the kernels.

To provide suitable material for a study of the time factor in relation to fertilization and kernel development, controlled pollinations were made, all of the plants for a given series of stages being hand-pollinated at one time. Thereafter samples were collected at the desired intervals. The age of the material in all cases was designated in terms of hours or days after pollination. Temperature relations were considered as an important factor influencing the rate of development, and seasonal variations also were studied in series of stages collected during three different growing seasons.

[4] RHOADES, V. H. A STUDY OF FERTILIZATION IN ZEA MAYS. Unpublished master's thesis, Cornell Univ. 1934.

[5] BEESKOW, H. C. THE SELECTIVE SEMIPERMEABILITY OF THE SEED COAT OF CORN. Unpublished master's thesis, Univ. Chicago. 1924.

[6] THARP, W. H., JR. INVESTIGATIONS UPON THE DEVELOPMENT, THE NATURE AND THE FUNCTION OF THE SEMIPERMEABLE MEMBRANE OF THE BARLEY KERNEL. Unpublished doctor's thesis, Univ. Wisconsin. 1932.

The method of preparing the material for microscopical study was as follows: Freshly harvested samples were fixed in a chromo-acetic acid mixture, containing 0.7 percent chromic acid and 1 percent glacial acetic acid, to 20 cc of which was added 3 drops of a 2-percent solution of osmic acid at the time of fixation. Paraffin sections 12μ to 15μ in thickness were prepared and stained, either with Flemming's triple stain or with Delafield's haematoxylin. Freehand sections of fresh and fixed material also were utilized, and in making determinations of the composition of the cell wall Sudan IV and certain other stains were employed.

DESCRIPTION

In the following account the essential features of the developmental morphology of the maize caryopsis are described. The investigation was concerned primarily with a study of embryogeny and the development of the endosperm and pericarp. However, an understanding of the changes which occur in the transformation of the ovary into the caryopsis requires a knowledge of the parts of the pistillate inflorescence which most directly are concerned in the development of the kernel. For this reason a brief description is first given of the mature pistillate spikelet, the ovary and ovule, and certain essential facts concerning pollination and fertilization. The structure of the entire caryopsis at different stages in development then is described, and this is followed by separate accounts of the developmental history of the embryo, endosperm, the integuments, the nucellar membrane, and the pericarp.

PISTILLATE SPIKELET

The morphology of the pistillate spikelet in maize has been described by Wigand (*55*), True (*47*), Guignard (*16*), Weatherwax (*50*), Miller (*30*), Stratton (*44*), and Arber (*2*). The spikelets ordinarily are borne in pairs arranged on the ear shoot or cob in double longitudinal rows. The total number of double rows on the ear usually ranges from four to eight, although higher numbers occur not infrequently. The individual spikelet normally has two flowers, of which the upper is functional and the lower aborted (fig. 1). But the reverse condition is sometimes found, especially near the tip of the ear. In kernels developed from the upper flower of the spikelet the embryo is on the side of the kernel toward the tip of the ear. When the lower flower develops the embryo is on the side of the kernel toward the base of the ear.

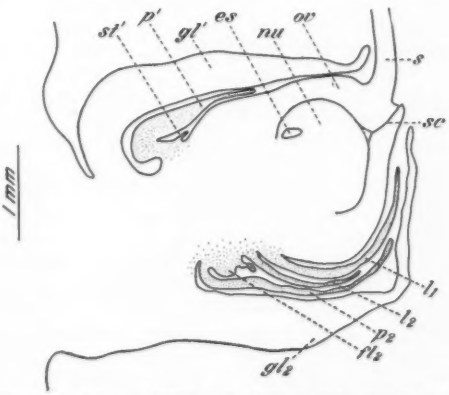


FIGURE 1.—Mature pistillate spikelet in radial longitudinal section: gl_1 and gl_2, Glumes subtending the spikelet; fl_2, aborted second flower; p_2 and l_2, palea and lemma of aborted flower; l_1, st_1, p_1, lemma, stamen, and palea of fertile flower; *es*, embryo sac; *nu*, nucellus of ovule; *ov*, ovary wall; *s*, style; *sc*, stylar canal.

A number of interesting special cases have been reported in which both flowers of the spikelet develop, producing paired grains, which are completely separate from one another, or double or connate grains resulting from some degree of fusion of the two flowers. In either case the members of the pair are arranged back to back, with the embryo of the upper grain on the side toward the tip of the ear and the embryo of the lower grain on the side toward the base of the ear.

Paired grains were first described in pod corn by Sturtevant (*45*), who noted exceptional instances of twin seeds in individual pods. Later, Kempton (*22*) reported a number of cases of inverted grains and was the first to interpret correctly their mode of origin. In Country Gentleman sweet corn the development of both flowers of the spikelet is the prevalent condition and is responsible for the crowded, irregularly spaced grains which characterize this variety (*43*, *49*).

Connate grains, made up of two kernels partially or completely united and enclosed in a common pericarp, were discovered by Kempton (*22*) in Hopi maize and in a hybrid between certain Chinese and Central American varieties. A strain of maize with many double and occasionally with triple grains, described by Blaringhem (*4*) as a new variety, *Zea mays* var. *polysperma*, was studied in the developmental stages by Stratton (*44*). It was found that in many instances both flowers of the spikelet were functional. Some developed separately as paired grains. Others fused more or less completely to form semiconnate or connate grains. Kernels of these types are compound structures, with embryos on opposite sides, and are not to be confused with simple grains having paired embryos on the same side of the kernel.

Another type of anomalous kernel development is represented by paired or twin embryos arranged side by side in an otherwise normal kernel. Such grains are found not infrequently in different stocks of maize, and the normal frequency of occurrence of this type of twinning is markedly increased by X-ray treatment. Since the pericarp and endosperm of these grains show no evidence of doubleness, the twin embryos presumably arise from a single embryo sac. Twin embryo sacs would be expected to produce twin endosperms as well as twin embryos. Furthermore, the twin plants produced by these kernels ordinarily are genetically identical, even in extremely heterozygous stocks, which indicates that they arise from a single zygote, presumably by a subdivision of the entire embryo or of that portion of it from which the plant develops, at some relatively early stage in ontogeny. Seedlings with two plumules and a single primary seminal root undoubtedly owe their origin to an incomplete separation of the embryo into two parts, a separation which involves only the portion which forms the plumule meristem.

The two flowers of the pistillate spikelet are partly enclosed by bracts, including a pair of empty glumes, and a lemma and palea associated with each flower in the positions indicated in figure 1. The upper fertile flower is essentially terminal with reference to the spikelet axis or rachilla. However, a rudimentary rachilla may be present, extending beyond the insertion of the fertile flower and between the paleae of the fertile and the sterile flower (*2*).

PISTIL

The functional pistillate flower in maize normally has a single pistil and three rudimentary stamens.[7] The pistil terminates in an elongated "silk", which properly may be referred to either as a stigma or a style, since it is receptive throughout its entire length but normally receives the pollen only at the tip. The basal portion of the pistil consists of a unilocular ovary containing a single highly specialized semianatropous ovule.

With respect to the extreme length of the style or silk, maize is unique among flowering plants. Ordinarily, the silk ranges in length from 10 to 30 cm, depending on the length of the ear shoot and the husks that envelop the ear and also upon the promptness with which pollination takes place after the silks are exposed. Normally, the silk ceases to elongate within approximately 24 hours after pollination, but, if pollination is deferred, elongation may continue for as long as a week or more and silk lengths of 50 to 75 cm may be attained under conditions favorable for growth.

The silk is branched at the tip and bears multicellular stigmatic hairs throughout its entire length. These hairs are very numerous at the tip and become progressively less numerous toward the base, where they are widely scattered. The silk is receptive throughout its entire length,[8] and normally remains so for a week or 10 days after it is first exposed.

The question of the fundamental structure of the pistil in *Zea* and other grasses has engaged the attention of morphologists for many years. The view that the grass pistil was derived from a single carpel was held by many early morphologists, including Schleiden (*37*), Hackel (*18*), and Engler (*11*), and is still adhered to by some modern investigators (*3*). Other early workers, including Roeper (*35*), Doell (*8*), Goebel (*13*), and Čelakovský (*7*), supported the view that three carpels are involved in the formation of the grass pistil, and this latter view is now generally accepted (*2*). The morphology of the maize pistil has been described by Schleiden (*37*), Wigand (*55*), Eichler (*9*), Poindexter (*33*), Walker (*48*), Schuster (*39*), Weatherwax (*53*), Arber (*2*), and others, and the tricarpellate nature of the pistil has been emphasized by most of these workers.

According to the interpretation of Schuster, the unilocular maize ovary consists fundamentally of three carpels united edge to edge. The single ovule is inserted near the base of the ovary on the side adjacent to the spikelet axis or rachilla in the region which represents, fundamentally, the fused margins of the two lateral carpels. The midrib bundles of the lateral carpels pass into the silk, and the fused marginal bundles of these lateral carpels supply the ovule. The third carpel is rudimentary, but a vestigial vascular trace, interpreted as the median bundle of this carpel, is sometimes present at the base of the ovary directly opposite the insertion of the ovule. The single style is obviously a double structure, presumably formed by a fusion of the styles of the two lateral carpels (*14*). This view is supported by the fact that the style is branched at the tip and has throughout its length

[7] In certain types of maize, notably dwarf and anther-ear types, fully developed stamens are present in both flowers of the pistillate spikelet (*10*).

[8] It is noteworthy in this connection that Mangelsdorf and Reeves (*29*) were successful in obtaining hybrids between *Zea* and *Tripsacum* by applying *Tripsacum* pollen directly to the base of maize silks after pollinations made in the usual manner had failed repeatedly to set seed.

a median constriction and that it has two vascular bundles with each of which is associated a strand of tissue interpreted as remnants of locular extensions of the two lateral carpels (*34*).

OVARY AND OVULE

The ovary at the time of fertilization is roughly spherical except in the region of the silk attachment, where it is somewhat elongated (fig. 2). Just below the region of silk attachment, on the side of the ovary away from the ear-shoot axis, there is a slight protuberance which marks the position of the stylar canal, so called by Guignard (*16*), who believed, wrongly, that the canal served to conduct the pollen tubes to the ovule. It is in this stylar-canal region that the margins of the ovary wall unite in ontogenetic development to enclose the ovarian cavity. The ovary wall at this stage is made up chiefly of thin-walled parenchyma cells capable of rapid growth by division and enlargement. The vascular tissue entering the base of the ovary supplies the ovule and subdivides to form the two prominent bundles of the silk and a varying number of rudimentary bundles in the lower portion of the ovary.

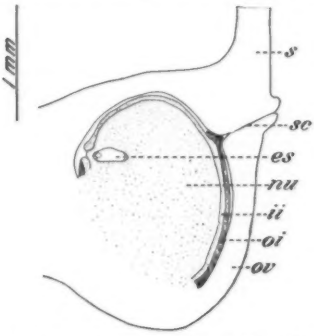


FIGURE 2.—Mature ovary in radial longitudinal section: *s*, Base of style; *sc*, stylar canal; *es*, embryo sac; *nu*, nucellus; *ii*, inner integument; *oi*, outer integument; *ov*, ovary wall.

The maize ovule at maturity is relatively large and virtually fills the ovarian cavity, as indicated in figure 2. In form it is definitely unlike any standard type, and represents an extremely modified condition variously referred to as semianatropous or modified campylotropous. The ovule has two integuments, a very broad insertion region, and no well-defined funiculus. The inner integument completely surrounds the ovule except at the micropylar orifice. The outer integument does not completely surround the ovule, being absent in a limited oval-shaped area extending from the micropyle in the direction of the silk-attachment region to the crest of the ovule. The embryo sac occupies a relatively small part of the nucellus in the micropylar region of the ovule.

POLLINATION AND FERTILIZATION

The sequence of events relating to the fertilization process in *Zea* from the time of pollination to the initiation of embryogeny and endosperm development has been described by Guignard (*16*), Weatherwax (*51*), Miller (*30*), and Rhoades,[9] and the main features of the process are well known. A consideration of the cytological details of fertilization was outside the scope of this investigation, but the time factor in relation to syngamy and the beginning of kernel development was carefully studied.

The pollen germinates almost immediately after it reaches the silks, as determined by direct microscopic examination of freshly ex-

[9] RHOADES, V. H. See footnote 4.

cised silk tips immediately after pollination. Within 5 minutes after the pollen was applied to the silks the pollen tubes emerged and were seen entering the central core of the multicellular stigmatic hairs, through which they passed into the main portion of the silk. In the early stages of pollen-tube growth, active protoplasmic streaming was noted repeatedly; the granular elements in the cytoplasm were seen to pass to and fro in the pollen tube and from the pollen grain into the pollen tube and back again. As the growth of the pollen tube continued, more and more of the granular material originally present in the pollen grain became localized in the pollen tube, and after 3 or 4 hours most of this granular material was no longer present in the pollen grain. The passage of the male gametes from the pollen grain into the pollen tube ordinarily takes place from 2 to 4 hours after pollination, and their movement into and along the pollen tube apparently is aided by the protoplasmic streaming. These observations were made at temperatures ranging from 22° to 25° C. At lower temperatures somewhat slower rates were noted, and at higher temperatures the rates were somewhat faster. These results are not in agreement with those of Miller and of Weatherwax, who stated that a few hours or at least 2 hours were required for germination to take place. However, Rhoades [10] and Sprague (*42*) reported that germination takes place soon after the pollen grains lodge on the silks.

The time interval between pollination and fertilization was found by Weatherwax (*51*) to be approximately 25 hours for silk lengths of about 25 cm. Miller (*30*) observed that ovules with silk lengths as great as 6 inches had been penetrated by the pollen tubes within 24 hours after pollination under ordinary field conditions. In plants maintained at a constant temperature of 25° C., Rhoades noted that the interval from pollination to fertilization was about 15 hours for silk lengths of 7 to 11 cm and about 17 hours for silk lengths of 11 to 14 cm. In the present investigations it was observed that in plants grown under field conditions at Ithaca, N. Y., with maximum day temperatures of 25° to 30° and minimum night temperatures of 13° to 17°, the interval was approximately 16 hours for silk lengths of 3 to 5 cm and 23 hours for silk lengths of 15 to 18 cm.

The fertilization of the egg and the polar nuclei by the male gametes takes place simultaneously, or nearly so, very soon after the pollen tube enters the embryo sac. An interval of 10 to 12 hours ordinarily intervenes between the fertilization of the egg and the first division of the zygote. The primary endosperm nucleus, however, undergoes division almost immediately after fusion is completed, and there are usually four or eight free endosperm nuclei present in the embryo sac when the fertilized egg divides.

TRANSFORMATION OF PISTIL INTO CARYOPSIS

The morphology of the pistil is profoundly altered during the development of the caryopsis. The ovule and its integuments are displaced by the developing embryo and endosperm, and there is little resemblance between the pericarp of the mature kernel and the ovary wall from which it was derived. The shape as well as the size of the caryopsis at maturity is very different from that of the pistil in the initial stages of kernel development. Before proceeding to give

[10] RHOADES, V. H. See footnote 4.

separate detailed accounts of the developing embryo, endosperm, and pericarp, the major morphological changes involved in the transformation of the pistil into the mature caryopsis will be outlined briefly.

The ovary in the initial stages of kernel development is nearly spherical in outline, and consists chiefly of thin-walled parenchyma cells capable of rapid growth. Within 3 or 4 days after pollination [11] a several-celled embryo embedded in cellular endosperm is well established in the nucellar tissue near the base of the ovule (fig. 3, *A*). At this stage the endosperm occupies an area not much greater than the space originally occupied by the embryo sac. The integuments

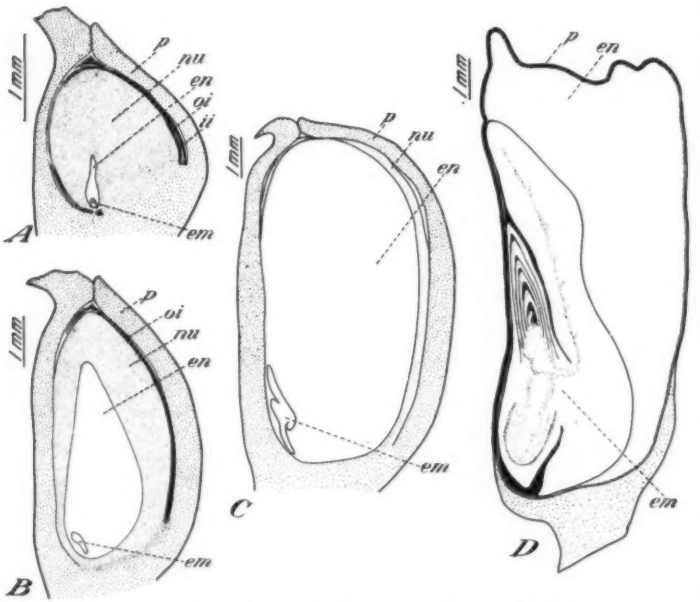


FIGURE 3.—Developmental stages in the transformation of the pistil into the caryopsis: *A*, 4 days after pollination; the embryo and endosperm have started to develop, but the structure of the ovary is essentially the same as at the time of fertilization. *B*, 10 days after pollination; the young caryopsis has enlarged considerably, the integuments are disappearing, and the endosperm is rapidly digesting away the nucellus of the ovule. *C*, 18 days after pollination; the caryopsis has continued to enlarge, the integuments have virtually disappeared, the nucellus is in the final stages of disappearance, and the compression of the pericarp in the crown region has begun. *D*, Morphologically mature kernel 45 days after pollination, consisting essentially of embryo, endosperm, and pericarp. The aleurone layer at the periphery of the endosperm is shown as a dotted line just inside the pericarp. The nucellar membrane between the aleurone layer and the pericarp is not shown in this drawing. *p*, Pericarp; *nu*, nucellus of the ovule; *oi*, outer integument; *ii*, inner integument; *en*, endosperm; *em*, embryo.

of the ovule are essentially intact, although disintegration of the inner integument has begun along the germinal face of the ovule. In this early period, from 2 to 5 days after pollination, there is a considerable enlargement of the entire ovary, unaccompanied by any appreciable change in form.

[11] The rates of development referred to throughout the paper are those which were typical of material collected under field conditions at Ithaca, N. Y., in 1924, and are based upon the examination of several kernels from each of 52 fixations taken at different intervals from fertilization to maturity. The ear shoots were hand-pollinated on Aug. 16 and the kernels were fully mature on Oct. 5. The rate for this particular season was intermediate between a somewhat more rapid rate of maturity noted during 1923 and a somewhat slower rate during 1926.

The period from 5 to 10 days after pollination is characterized by a pronounced elongation of the young caryopsis and by a rapid growth of the endosperm. A 10-day stage is illustrated in figure 3, *B*. The ovary wall has increased rapidly in length and to a lesser extent in width. Scattered nuclei surrounded by remnants of cytoplasm are all that remain of the inner integument over the germinal face of the ovule, but at the top and over the abgerminal face the inner integument is still intact. The outer integument is starting to disintegrate at the abgerminal attachment region and in the region of the stylar canal. The embryo is still relatively small, but the endosperm has expanded until it occupies approximately one-half of the nucellus, which itself is about twice as wide and three times as long as it was at the time of fertilization.

The growth of the entire kernel continues at a very rapid rate during the 10- to 20-day period, as shown by the following data from measurements of the length of the caryopsis taken at 5-day intervals from the time of pollination to maturity:

Age of material (days):	*Length of kernel (millimeters)*
0	1. 5
5	2. 5
10	4. 5
15	6. 5
20	8. 0
25	9. 0
30	10. 0
35	11. 0
40	11. 5
45	11. 5
50	11. 5
55	11. 0

The endosperm increases several times in volume and in so doing encroaches upon and digests away the nucellus, which has been displaced, except in a very limited peripheral area, at the end of 18 days (fig. 3, *C*). At this stage the integuments, except at the stylar-canal region, have disappeared as definite layers of tissue, leaving here and there only scattered masses of disintegrating protoplasts between the inner epidermis of the pericarp and the outer epidermis of the nucellus. The pericarp has now reached its maximum thickness, and in the crown region a collapse of the inner cells has taken place, a process which later extends throughout the extent of the pericarp and partly accounts for the very appreciable reduction in thickness as maturity is reached. In the embryo the main plumule-radicle axis is fully differentiated, but the rate of growth of the embryo during this period is relatively slow in comparison with the much more rapid growth of the endosperm.

During the latter part of the developmental period in the formation of the caryopsis the most conspicuous morphological changes are an extensive enlargement of the embryo, further increase in the size of the endosperm and the differentiation of its epidermis into the aleurone layer, the complete disappearance of the nucellus with the exception of the outer wall of the epidermal cells, and the reduction of the pericarp to a thin lignified layer surrounding the caryopsis (fig. 3, *D*). The growth of the embryo is most rapid from about 20 to 40 days after pollination (table 1). The enlargement of the endosperm and pericarp in the final stages is brought about chiefly by an increase in cell size;

cell-division activity is relatively slight after about 45 days. The caryopsis attains its maximum size at 40 to 45 days and is morphologically mature, except for some further growth of the embryo. At this time the grain passes from the so-called "soft-dough" to the "hard-dough" stage. After approximately 45 days the growth of the embryo normally ceases.[12] During the next 5 or 10 days the crown region of the kernel becomes indented and by the end of 50 or 55 days the caryopsis has assumed the typical mature form.

TABLE 1.—*Rate of growth of the embryo as determined by length measurements during development*

Age of embryo (days)	Length of embryo	Increase in length	Age of embryo (days)	Length of embryo	Increase in length	Age of embryo (days)	Length of embryo	Increase in length
	Mm	*Mm*		*Mm*	*Mm*		*Mm*	*Mm*
5	0.1		20	2.7	1.3	50	8.1	1.6
10	.4	0.3	30	4.5	1.8	55	8.4	.3
15	1.4	1.0	40	6.5	2.0			

EMBRYOGENY

The development of the embryo in maize has received little attention. Weatherwax (*52*) outlined the course of development very briefly. Other workers have concerned themselves chiefly with the mature embryo for the purpose primarily of determining the homologies of the scutellum, coleoptile, nodes, etc., in relation to those of other grasses. An extensive critical review of the literature has been prepared,[13] and a summary of the various conflicting views pertaining to this highly controversial subject has been published, by McCall (*26*). The present account is limited to a consideration of the ontogenetic development of the embryo.

The two-celled embryo, formed by the division of the fertilized egg or zygote (fig. 4, *B*), consists of a small lenticular apical cell and a much larger basal cell (*C*). This division of the zygote occurred from 30 to 34 hours after pollination under the conditions that prevailed during the growth period of the material used in these studies, i. e., with maximum day temperatures of 25° to 30° C., minimum night temperatures of 13° to 17°, and silk lengths of 12 to 18 cm. In plants maintained at a constant temperature of 25° and with silk lengths of 10.5 to 14.5 cm, Rhoades [14] obtained two-celled embryos 28 to 30 hours after pollination. In the present study embryos with three or four cells were noted at 36 hours (*E–G*), and at 42 hours the apical cell ordinarily had divided twice, and two or three divisions had occurred in the subapical portion (*H–N*). Four days after pollination the embryos contained ordinarily from 10 to 24 cells (*O–Q*).

Especially noteworthy in connection with the early history of the maize embryo is the fact that the proembryo develops very irregularly with no very definite or orderly arrangement of the cells or sequence of cell divisions. In most grass embryos previously described, it has

[12] In certain unusual cases, described as "premature germination" (*27, 28*) or "vivipary" (*12*), continuous development of the embryo takes place without the normal intervention of a rest period.

[13] MCCALL, M. A. REVIEW OF LITERATURE ON THE MORPHOLOGY AND HOMOLOGIES OF THE GRASS EMBRYO. Typewritten manuscript, U. S. Department of Agriculture Library. Washington, D. C. 1934.

[14] RHOADES, V. H. See footnote 4.

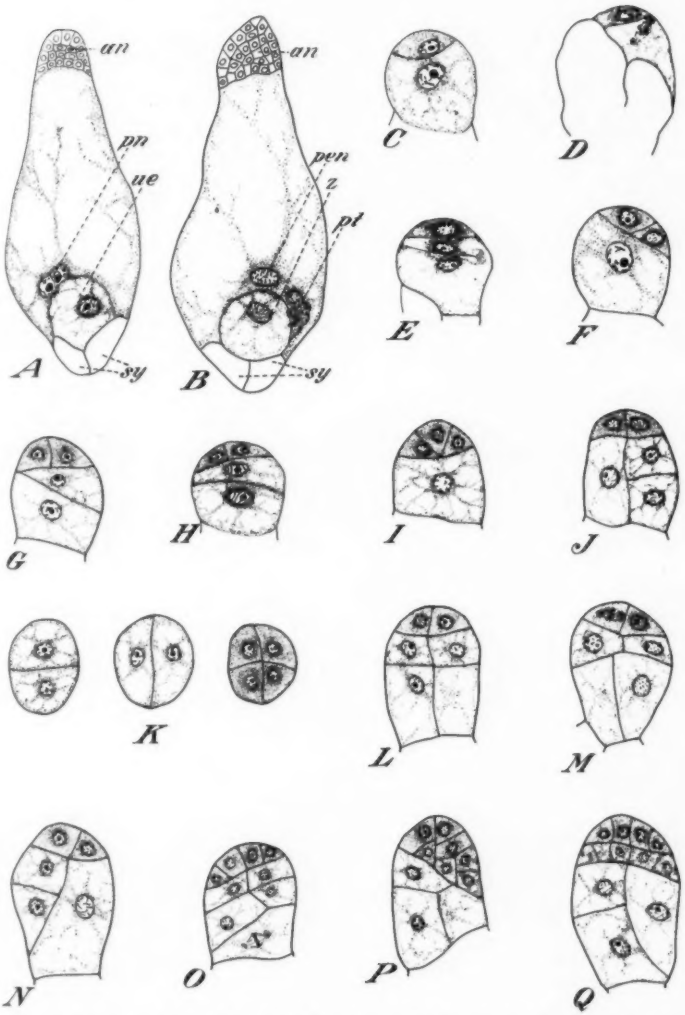


FIGURE 4.—Embryo sacs before and after fertilization, and initial stages in the development of the proembryo illustrating the varying position and sequence of the cell walls. *A*, Embryo sac before fertilization: *an*, Antipodals; *pn*, polar nuclei not yet fused; *ue*, unfertilized egg; *sy*, synergids. *B*, Embryo sac after fertilization: *an*, Antipodals; *pen*, primary endosperm nucleus; *Z*, zygote (fertilized egg); *pt*, pollen-tube remnant; *sy*, synergids. *C* and *D*, Two-celled proembryos 32 hours after pollination. *E–G*, Three- and four-celled stages 36 hours after pollination. *H–N*, Stages observed 42 hours after pollination. *O–Q*, Proembryos with 10 to 24 cells, 4 days after pollination. All figures are from radial longitudinal sections except those of *K*, which are cross sections from the base to the tip of a stage similar to *H*, *A*, *B*, × 200; *C–H* × 225.

been stated that tiers of three or four cells with parallel cross walls are formed in a regular manner, and that there is a very definite sequence of cell divisions in the initial stages (*3*, *38*, *41*). In *Zea*, fairly regular tiers of cells occasionally are produced (fig. 4, *E*, *H*, *O*), but more frequently the arrangement is quite irregular (*G*, *I*, *P*) and the order in which the cells divide is inconstant. The proembryo of maize does not regularly conform to any definite growth pattern.

During the period from 4 to 8 days after pollination the growth of the proembryo is limited chiefly to the apical region (fig. 5). In the basal or suspensor region few cell divisions occur. As a result of the relatively much greater cell-division activity in the upper portion, the embryo develops into a club-shaped structure (fig. 5, *C–H*). The original cell boundaries, which at an earlier stage subdivided the embryo longitudinally into three or four parts of unequal size, may be identified readily as late as 4 to 6 days after pollination (*A–C*). Thereafter, they are identified with difficulty or not at all, and it is impossible to detect in the later stages the regions that originated

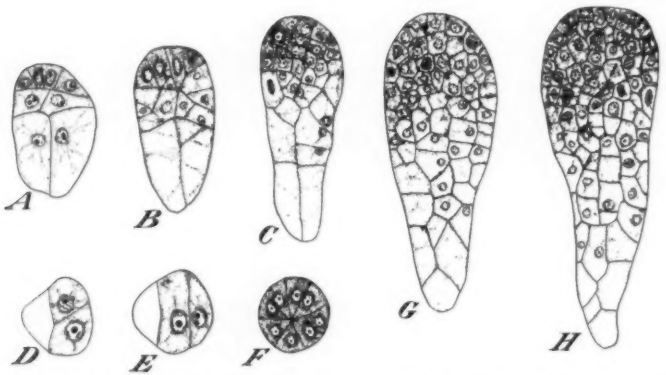


FIGURE 5.—Proembryos 4 to 8 days after pollination. In radial longitudinal section: *A*, 4 days; *B*, 5 days; *C*, 6 days; *G*, 7 days; *H*, 8 days. *D–F*, Transverse sections from the base to the tip of a 4-day embryo. *A–C*, *G*, *H* × 225.

from any of the original sectors of the very young embryo. Except for the localization of growth, primarily in the upper portion, the proembryo is wholly undifferentiated up to and including the seventh day (*G*); at the periphery of the embryo both anticlinal and periclinal walls are formed, and elsewhere cell divisions occur at random without definite orientation of the daughter cells. A pronounced decrease in size accompanies the rapid increase in the number of cells during this period, and the relatively large, irregularly shaped cells of the 5-day embryo are replaced subsequently by smaller isodiametric cells.

Beginning approximately 8 days after pollination, differentiation progresses rapidly in the embryo. At this time a definitive epidermis makes its appearance over the apical region (fig. 6, *A*); later it extends gradually down the sides of the embryo toward the region occupied by the suspensor (*B*). Cell-wall formation becomes chiefly anticlinal in the epidermal tissue as differentiation progresses, and the production of periclinal walls, noted frequently in the peripheral

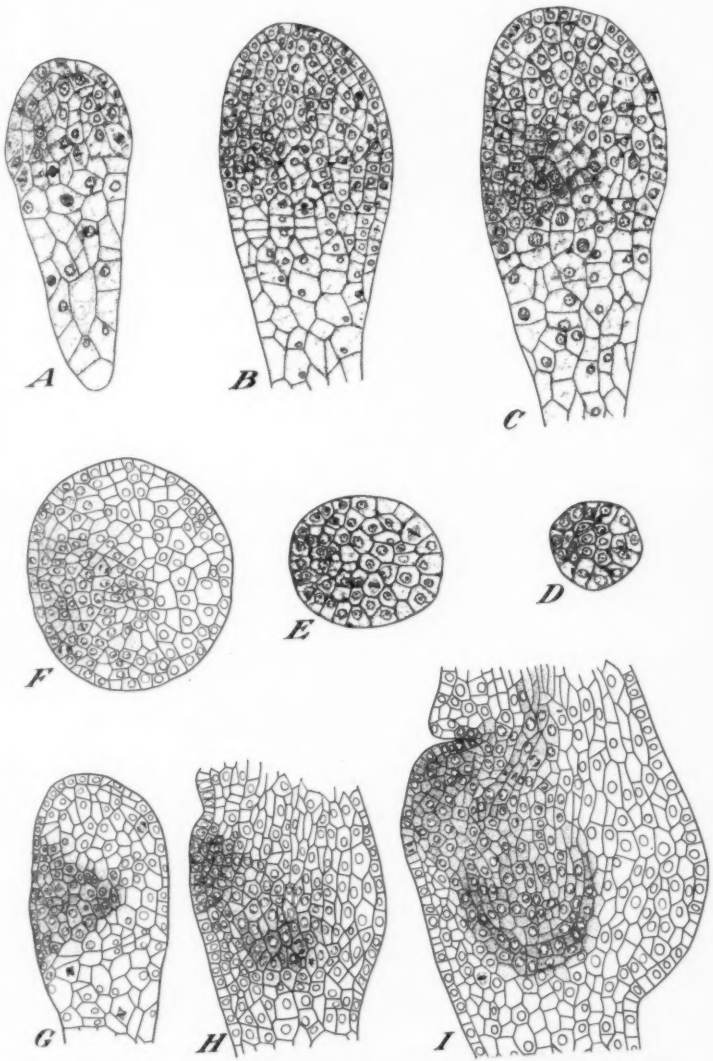


FIGURE 6.—Embryos 8 to 13 days after pollination, showing stages in the differentiation of the epidermis and the permanent plumule-radicle axis of the more mature embryo: *A–C*, Radial longitudinal sections showing stages at 8, 9, and 10 days after pollination; epidermis differentiating over the tip of the embryo in *A* and *B*. *C*, Initial stage in the differentiation of the plumule-radicle axis as a wedge-shaped group of cells in the anterior portion of the embryo. *D–F*, Transverse sections in the subapical region of embryos, 6, 7, and 10 days after pollination, showing stages in the differentiation of the epidermis and axis of the more mature embryo. *G–I*, Radial longitudinal sections of the subapical portion of embryos, 10, 12, and 13 days after pollination, illustrating in *H* and *I* the manner in which the stem and root portions of the plumule-radicle axis become differentiated from the single group of meristematic cells shown in *G*. *A–F*, × 200; *G–I*, × 175.

cells during the earlier stages (*A*), becomes relatively infrequent as the embryo matures. Another type of differentiation observed at about this stage consists in a marked tendency for the cells in the subapical region of the proembryo to divide actively, with the new cell walls forming at right angles to the axis of the embryo (*A*). Groups of cells with parallel cross walls are thus formed between the suspensor region and the tip of the embryo (*B*). In this manner the longitudinal extent of the meristematic tissue in the upper portion of the embryo is materially increased. This is obviously a preliminary step in the differentiation of the main axis of the more mature embryo, an axis which does not coincide with the axis of the proembryo.

The axis of the more mature embryo is first recognizable 9 or 10 days after pollination as a group of densely protoplasmic and actively dividing cells at the front (anterior face) of the embryo, slightly below the tip. This group of cells is roughly triangular when viewed either in radial longitudinal section (fig. 6, *C*), or in cross section (*F*). The rate of growth within this group of cells is more rapid than in the other parts of the embryo, and as a result a slight protuberance soon develops on the anterior face of the embryo (*G*, *H*), a stage which is ordinarily reached approximately 10 days after pollination. At 12 days this protuberance is noticeably enlarged (*H*). At 13 days it has increased still further in size, and the single group of meristematic cells previously formed has now differentiated into two distinct groups (*I*). Of these, the upper group with reference to the embryo axis is closely associated with the outgrowth or protuberance on the face of the embryo and is the primordium of the stem portion of the new axis; the lower group is the primordium of the corresponding root portion. Associated somewhat more closely with the former than with the latter primordium is a strand of elongated cells, which is the forerunner of the main vascular supply to the scutellum. Within the lower or root primordium certain cells very early assume a definite orientation, anticipating the delimitation of the coleorhiza and primary seminal root.

A clearer picture of the relative position of the differentiating axis of the more mature embryo in relation to the axis of the proembryo may be obtained from the illustrations in figure 7, *A–D*, which are reproduced at a relatively low magnification and show the form of the entire embryo at 10 to 14 days. This differentiating axis is a lateral structure oriented in an oblique position with reference to the longitudinal axis of the embryo (*B–D*). With the appearance of the new axis there is a pronounced shift in the polarity of the embryo, from an essentially vertical to a definitely oblique orientation, and the major growth activity during the later stages of embryogeny is centered about the differentiating plumule-radicle meristem. However, there is also an appreciable amount of growth in the suspensor region, particularly at 13 and 14 days (*C*, *D*); and in connection with the development of the scutellum there is a gradual and extensive enlargement both in the region which was formerly the tip of the proembryo and along the posterior side above the suspensor region. Figure 7, *C* and *D*, in comparison with *B*, shows the extent of growth during those stages in the suspensor and scutellum regions.

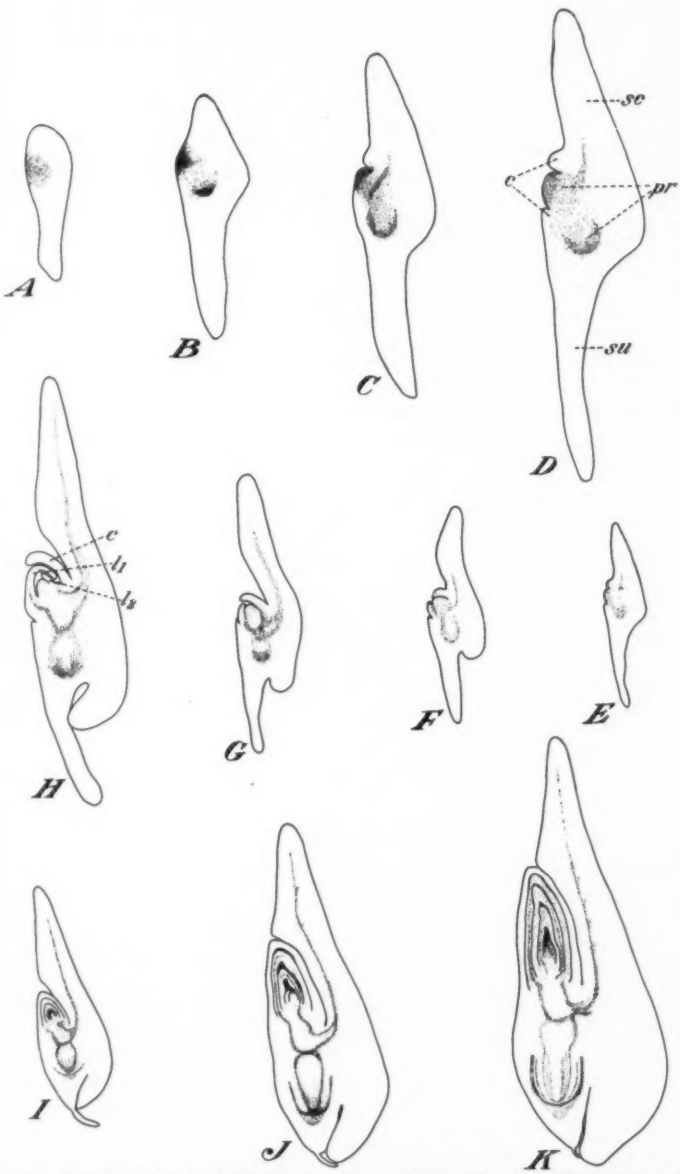


FIGURE 7.—Outline drawings of embryos in radial longitudinal section, 10 to 45 days after pollination, showing changes in shape and size and relative positions of different parts: *A–D*, Stages at 10, 12, 13, and 14 days, showing position of the differentiating plumule-radicle axis with reference to the suspensor and differentiating scutellum: *sc*, Scutellum; *pr*, plumule-radicle axis; *su*, suspensor; *c*, coleoptile primordium. *E–H*, Stages at 14, 16, 18, and 20 days after pollination, showing continued development of the axis and the scutellum, relatively little further growth of the suspensor, and the appearance of the primordia of the first seedling leaves: *c*, Coleoptile; l_1 and l_2, primordia of first and second seedling leaves. *I–K*, Stages at 25, 35, and 45 days after pollination; the plumule-radicle axis and the scutellum become much enlarged, the suspensor persists merely as a vestigial organ, and additional seedling leaves appear; *K*, essentially mature embryo. *A–D*, × 60; *E–H*, × 25; *I–K*, × 12.

During the period from 14 to 20 days after pollination the primordia of the coleoptile and first seedling leaves make their appearance (fig. 7, *E–H*). The coleoptile is formed initially as a ridge of tissue which nearly surrounds the central stem meristem (*D*, *E*). This ridge develops more rapidly above than below the central meristem and at a relatively early stage assumes the form of a sheathing structure that envelops the stem tip and the embryonic seedling leaves. The first seedling leaf arises below the stem meristem as a ridge of tissue similar to and opposite that of the coleoptile primordium, and the second leaf appears subsequently above the stem meristem directly opposite the first leaf (*H*).

Additional seedling leaves continue to form during the period from 25 to 45 days after pollination, the total number present at maturity usually being five, and the radicle with its ensheathing coleorhiza becomes fully differentiated during this period (fig. 7, *I–K*). There is also a general enlargement of the entire plumule-radicle axis and a corresponding increase in the dimensions of the scutellum. The suspensor ceases to enlarge after 20 days and thereafter persists apparently as a nonfunctional and unimportant part of the maturing

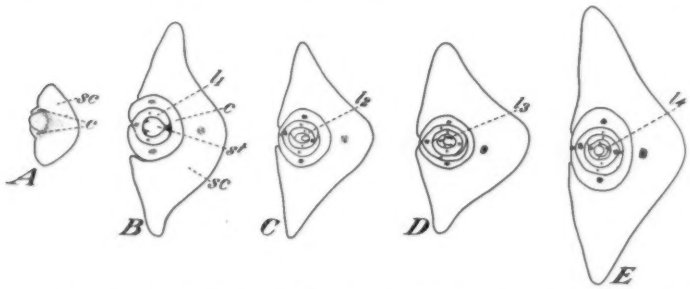


FIGURE 8.—Cross sections in the stem-tip region of embryos: *A–E*, 16, 20, 25, 35, and 45 days after pollination: *sc*, Scutellum; *c*, coleoptile; *st*, stem tip; l_1–l_4, successive seedling leaves; *A*, *B*, × 25; *C–E*, × 12.

embryo (*I–K*). As previously stated, the growth of the embryo as a whole is very rapid from 20 to 40 days after pollination, and the drawings *I* to *K*, which are of the same magnification, graphically illustrate this fact.

The relative position of the axis of the older embryo changes gradually in the later stages of maturity. At first the axis is definitely oblique (fig. 7, *D*), but later it assumes a position nearly parallel to the remainder of the embryo (fig. 7, *K*). It is also noteworthy that the scutellum essentially surrounds the axis of the embryo at maturity. This relationship is clearly shown in cross sections of the embryo at the level of the stem tip (fig. 8, *A–E*). These cross-section views also show the relative positions of the coleoptile and plumule leaves and the main vascular bundles supplying these structures and the scutellum.

The embryo is morphologically mature approximately 45 days after pollination, except for some additional development of the seedling leaves, of which there are normally five present in the ripe grain, and a slight increase in size throughout the embryo. The vascular tissues become more fully developed in the final stages of embryo formation, and a specialized epidermal tissue forms along

the posterior face and at the base of the scutellum. This specialized tissue serves a haustorial and secretory function as the embryo and seedling obtain nourishment from the endosperm.

ENDOSPERM FORMATION

The development of the endosperm begins almost immediately after fertilization, as described by Guignard (*16*), Weatherwax (*52*), and Rhoades.[15] The primary endosperm nucleus (fig. 4, *B*), which

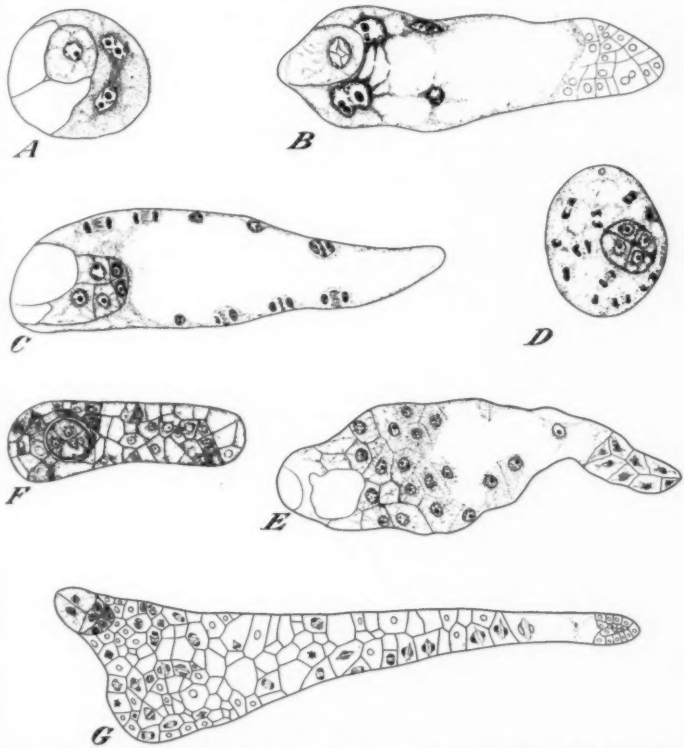


FIGURE 9.—Initial stages in the development of the endosperm: *A*, Cross section of the embryo sac at the level of the fertilized egg, showing the daughter nuclei formed by the division of the primary endosperm nucleus, 26 hours after pollination; *B*, longitudinal section of embryo sac 34 hours after pollination, showing zygote and eight-nucleate stage of free endosperm development, not all of the nuclei being shown in the figure; *C*, longitudinal section showing free endosperm nuclei in division, passing from the 128- to the 256-free-nucleate stage, 3 days after pollination; *D*, cross section of same stage as *C*; *E*, oblique longitudinal section of endosperm passing from free-nucleate to cellular phase, 3½ days after pollination; *F*, cross section of cellular endosperm in the region of the embryo, 4 days after pollination; *G*, median longitudinal section view at the same stage. *A*–*F*, × 175; *G*, × 80.

is formed by the fusion of the second male nucleus with one polar nucleus and the subsequent union of the product of this fusion with the second polar nucleus (*30*),[15] divides within 2 to 4 hours after the fusion is completed. The daughter nuclei then migrate to opposite sides of the embryo sac in the basal (micropylar) region adjacent to

[15] RHOADES, V. H. See footnote 4.

the zygote (fig. 9, *A*). Within the 12-hour period following syngamy, i. e., within approximately 36 to 48 hours after pollination under the conditions which prevailed while these studies were in progress, a second, and frequently a third, division takes place, and the resulting four or eight free endosperm nuclei thus formed are distributed about the periphery of the micropylar end of the sac (*B*). Three days after pollination approximately 128 free endosperm nuclei are present, which is the number to be expected after seven nuclear divisions. Noteworthy in this connection is the fact that there is a very definite tendency for the divisions to occur in unison among the free endosperm nuclei (*C*), and this tendency persists even after the endosperm has become cellular (*G*). As the nuclei multiply, migration in the direction of the antipodal region of the sac continues and thus the entire embryo-sac cavity gradually becomes lined with nuclei.

The rapidity with which the endosperm begins to form is in marked contrast to the slower progress of embryogeny in the initial stages. Four to eight free endosperm nuclei are present at the time the fertilized egg divides, and when the embryo reaches the 6- to 8-cell stage there are from 128 to 256 free endosperm nuclei (fig. 9, *C*).

The developing endosperm passes gradually from the free-nucleate to the cellular phase, beginning about 3½ days after pollination. Cell-wall formation is initiated in the region of the endosperm surrounding the embryo and progresses in the direction of the antipodal cells (fig. 9, *E*). At 4 days the endosperm ordinarily is completely cellular except in the antipodal portion, and the middle region previously occupied by a large central vacuole becomes filled with cellular endosperm (*G*). When examined in cross-section view, that is, in a plane approximately at right angles to the axis of the proembryo, the endosperm in the micropylar region surrounding the embryo is at this stage very much flattened laterally and is only three or four cells in thickness (*F*). In the direction of the antipodals, however, the endosperm is much thicker.

The external form of the endosperm changes materially as it develops and there is also a tremendous increase in size. The length of the mature endosperm is approximately 50 times as great as it is in the initial stages and there is a corresponding increase in width. Before the histological features of growth and differentiation in the endosperm are described, the gross changes in external morphology will be outlined briefly.

The size and shape of the endosperm at different stages in development are shown in figure 10. In the early stages, up to 12 or 15 days, the enlargement of the endosperm is more rapid in the basal (micropylar) region than it is in the apical (antipodal) region (fig. 10, *A–F*). At 24 days the apical region is as large as or larger than the basal region (*G*), and in the later stages the former increases more rapidly than the latter.

The endosperm begins to elongate very rapidly, beginning 2 to 3 days after pollination (fig. 10, *C*). As this elongation takes place the antipodal cells retain their position at the apex of the endosperm tissue. As the endosperm increases in size the nucellar tissue immediately surrounding it is digested away and permits the growing endosperm to expand freely. At 2 days the approximate length of the endosperm is 0.3 mm, at 8 days 2 mm, at 24 days 10 mm, and at 48 days 15 mm; and there is a comparable increase in the diameter of the endosperm

FIGURE 10.—Outline drawings showing changes in the size and shape of the embryo and endosperm at different stages of maturity; also position of the antipodal tissue at the tip of the endosperm in longitudinal sections. Radial longitudinal sections at top; cross sections below, at the level of the embryo (*a*) and at a level near the tip of the endosperm (*b*), as indicated in the longitudinal sections. The age of the different members of the series in days after pollination is as follows: *A*, 1½; *B*, 2; *C*, 3; *D*, 4; *E*, 8; *F*, 12; *G*, 24; *H*, 36; *I*, 48.

during the same period. The dimensions of the endosperm in planes of section at right angles to the longitudinal axis are portrayed in the cross-section drawings of figure 10. One of the series of sections illustrated (series *a*) was from the level at the tip of the embryo and the other (series *b*) was from the region near the tip of the endosperm. The shape of the endosperm in cross section, as illustrated by these figures, is oval, or roughly so, in most stages of development. However, in the early stages the extent of the endosperm is much greater in the germinal-abgerminal direction than it is in the longitudinal plane at right angles to this (*A–F*), while in the later stages (*G–I*), because of the crowding of the kernels on the ear, this condition is reversed and the width is greater than the germinal-abgerminal thickness of the endosperm.

The internal differentiation of the endosperm was studied cytologically from the time it passed from the free nucleate to the cellular condition until it reached maturity, in order to determine as accurately as possible the manner in which growth and specialization take place within the endosperm. Just as in the case of the young embryo, the endosperm in the early stages is essentially undifferentiated and consists of thin-walled parenchyma cells of varying size and shape. There is at first no specialized epidermal layer and cell-division activity is general throughout the entire tissue, including both the marginal and the central cells (figs. 9, *G*, and 11, *A*). Gradually there is a tendency for cell division to be localized chiefly in the peripheral zone (fig. 11, *B–F*) and the growth of the inner region is primarily by increase in the size rather than in the number of cells.

There are several layers of cells in the peripheral region of the endosperm that are involved in the cell-division activity during the period from 12 to 16 days after pollination (fig. 11, *D–F*). In the epidermal layer of cells periclinal wall formation takes place repeatedly as development proceeds, and in the underlying cells additional divisions occur in the same plane. Rows of cells are thus formed which extend inward toward the central region of the endosperm (*E, I*). This arrangement of cells in fairly definite radial rows closely resembles the arrangement produced by cambial activity in the formation of secondary tissues.

The cambiumlike activity described above involved the epidermal layer of cells up to the 16- or 18-day stage along the germinal face of the endosperm (fig. 11, *G*), and for 3 or 4 additional days along the abgerminal face of the endosperm. In the crown region and in the basal region of the endosperm there was relatively little meristematic activity during this period; the cells in this region were relatively large and presented the appearance of a well-differentiated tissue. It is probable that this basal tissue functions actively in the transfer of nutrients from the vascular tissue of the caryopsis to the developing endosperm and embryo, as Weatherwax (*54*) and Lampe (*25*) have suggested. The cytological observations which were made to determine the manner of growth throughout the endosperm did not confirm the statement of Lampe (*25, p. 353*) that cell-division activity is more prolonged in the basal region than it is elsewhere. In fact, the reverse condition was noted in the different stocks examined, namely, that cell-division activity ceased first in the basal region and was much more prolonged at the periphery of the middle portion between

the base and the crown region of the endosperm. It is possible that the endosperm develops in a different manner in other varieties of maize.

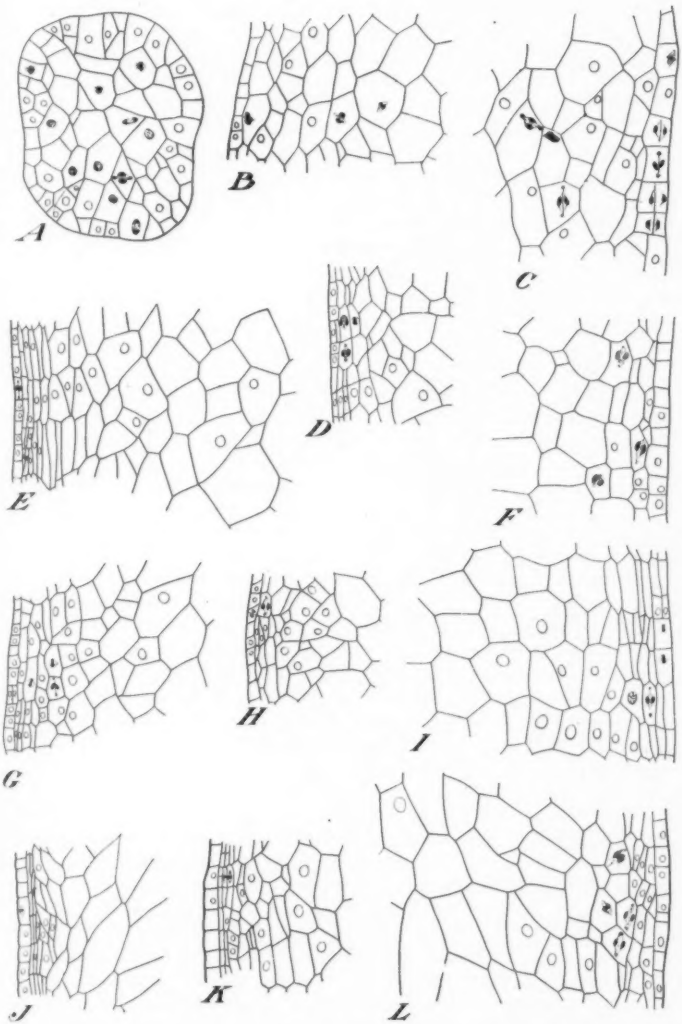


FIGURE 11.—Cellular structure of the endosperm from different regions of kernels at intervals of 6 to 21 days after pollination, showing manner of growth and progress of differentiation. *A*, Cross section from middle portion of the endosperm at 6 days. *B–F, G, I, J, L*, Radial longitudinal, and *H, K*, cross sections from germinal and abgerminal regions of the endosperm at a level just above the embryo; figures with the epidermal layer to the left are from the germinal portion and those with the epidermis to the right are from the abgerminal portion of the endosperm. The age of the endosperm in days after pollination is as follows: *B*, 9; *C*, 11; *D*, 12; *E* and *F*, 16; *G–I*, 18; *J–L*, 21. During the developmental period represented by these figures the epidermis of the endosperm, which later becomes the aleurone layer, is differentiated. × 125.

The epidermal layer of endosperm cells almost entirely ceases its meristematic activity in the germinal region approximately 18 days after pollination and at 20 to 22 days in the abgerminal region (fig. 11, *J–L*). This layer then assumes the characteristics of a distinct epidermal tissue; subsequent growth is almost exclusively by anticlinal wall formation and by cell enlargement. This epidermis in the definitive state is the aleurone layer of the morphologically mature endosperm. Meristematic activity persists in the subepidermal tissue until about 45 to 48 days after pollination; the cells in this region remain relatively small in comparison with the much larger cells in the epidermal, or aleurone, layer, and cambiumlike rows of cells continue to form as late as 48 days after pollination in the anterior and posterior regions of the endosperm (fig. 12, *E* and *F*). In the final stages of endosperm development these subepidermal cells cease their division activity and increase markedly in size (fig 12, *G* and *H*). Occasional cell divisions occur in the aleurone layer, especially in the region extending over the face of the embryo, during the final stages of endosperm development.

ANTIPODAL TISSUE

At the time of fertilization in maize the embryo sac contains a varying number of antipodal cells, usually ranging from 24 to 48, grouped together in the end of the sac opposite the egg cell and the synergids (pl. 1, *A*). The antipodals are relatively small, chiefly uninucleate cells. They constitute a haploid tissue having the same genetic constitution as the egg cell, since both are derived from a single megaspore (*51*). In many grasses other than maize, the antipodals disintegrate soon after endosperm formation begins, and it was formerly believed that a similar type of behavior characterized the antipodals in *Zea* (*30*, *51*). Later Weatherwax (*53*) reported that groups of antipodal cells had been observed in nearly mature kernels.

During the course of the present study, in which the development of the caryopsis was traced in a close series of stages, the presence of antipodal tissue was noted at all stages from fertilization to maturity. The antipodal cells not only persist but in many instances retain the capacity to divide, and as kernel development proceeds there may be an appreciable increase in the amount of antipodal tissue. Typical mitotic nuclear divisions were observed not infrequently, and in some of these the typical haploid number of 10 chromosomes was identified.

The frequency of occurrence of antipodal tissue in the advanced stages of kernel development was determined by a microscopical examination of serial longitudinal sections of caryopses from the commercial maize variety Pride of Michigan. Antipodal tissue was definitely identified in 28 of 52 caryopses examined. A similar examination of a smaller number of kernels from other varieties and genetic cultures suggested that there may be a considerable amount of variation in the frequency with which the antipodal tissue persists in different stocks of maize. An explanation of the absence of the antipodals in many nearly mature kernels was obtained by tracing their developmental history in the earlier stages of kernel development.

During the first 4 to 6 days after pollination the antipodals were present in all the ovules examined. Throughout this period they retained the same general appearance that they presented at the time of fertilization (pl. 1, *A* and *B*); there was little or no evidence

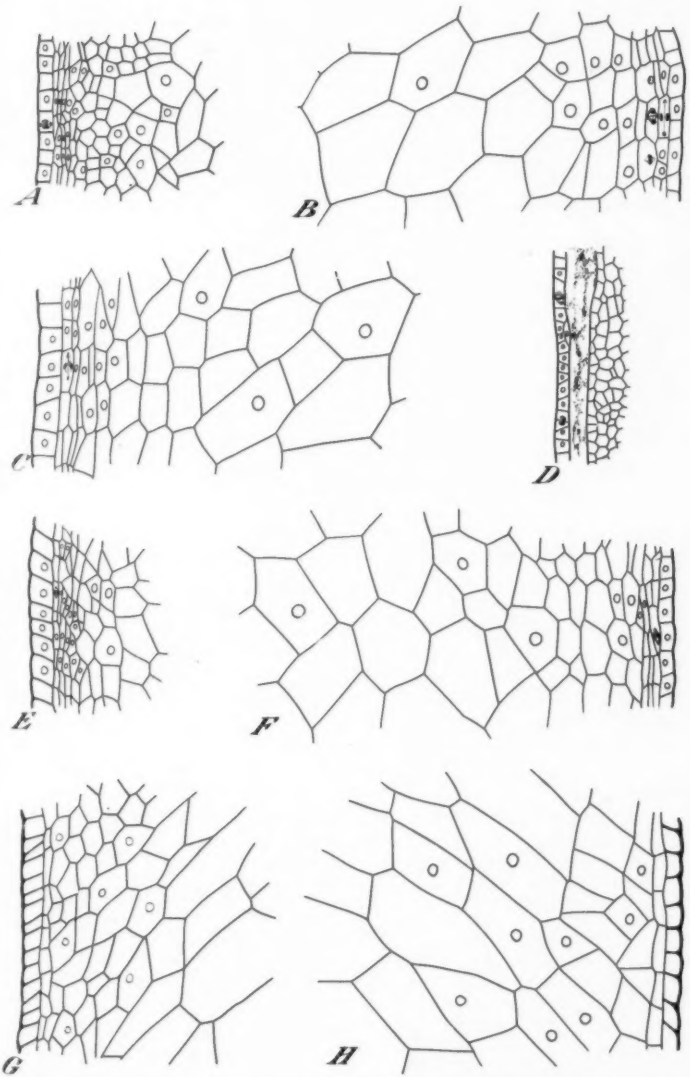


FIGURE 12.—Cellular structure of the endosperm as it approaches maturity, showing regions of the endosperm comparable to those in figure 11: *A* and *B*, 26 days; *C* and *D*, 36 days; *E* and *F*, 48 days; *G* and *H*, 55 days; in *D* the epidermal or aleurone layer of the endosperm is shown extending over the face of the scutellum tissue of the embryo. *A*, *B*, *E* are from cross sections and *C*, *D*, *F*–*H* are from radial longitudinal sections. × 125.

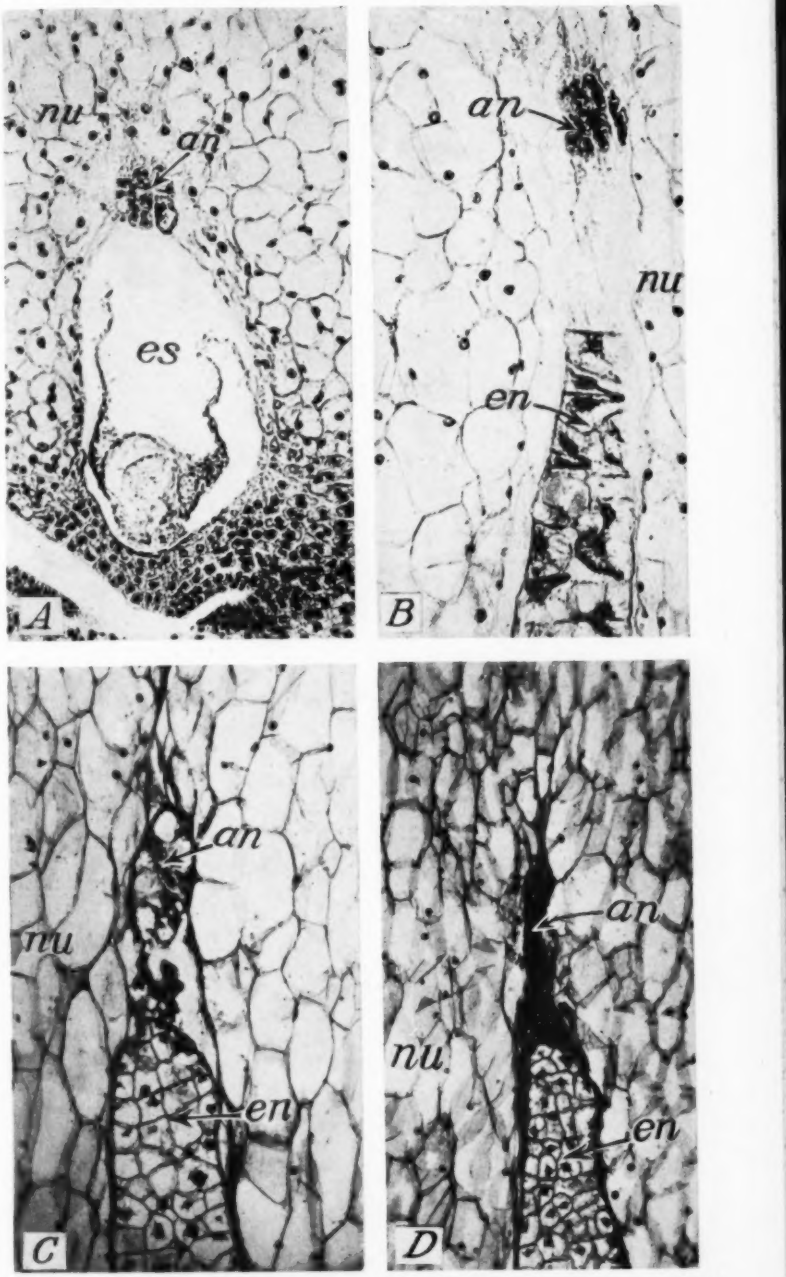
either of growth by cell division or of disintegration. However, the position of the antipodal tissue within the nucellus changed appreciably during this period, a change brought about by a translocation of the antipodals away from the micropylar region into the deeper lying tissues of the nucellus. This change in the position of the antipodal tissue occurred concomitantly with the development of the endosperm in the same general direction. The distance traversed by the antipodals during this period of migration was roughly equivalent to from 2.5 to 3 times the longitudinal extent of the embryo sac at the fertilization stage (cf. fig. 9, *B* and *G*).

The change in the position of the antipodal cells and the enlargement of the developing endosperm were facilitated by the disintegration of the nucellus adjacent to these tissues (pl. 1, *B*). The nucellar tissue is not crushed and compressed by the expanding endosperm and antipodals but becomes disorganized and gradually disappears, presumably being digested away and eventually resorbed through enzyme activity.

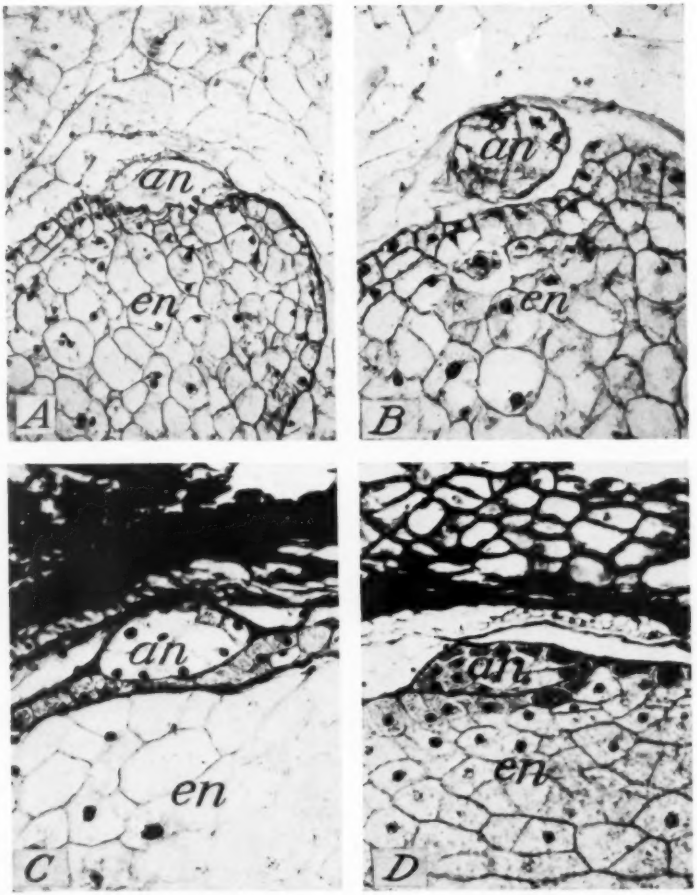
Initial stages in the disintegration of the antipodal tissue were noted at about 6 days after pollination (pl. 1, *C*), and more advanced stages were noted a few days later (*D*). Along with these cases in which disorganization of the antipodals was in progress, a larger number of cases were noted in which there was no evidence of disintegration.

At 10 to 12 days after pollination ovules were observed in which the antipodals had disappeared, but the space the antipodal tissue had occupied often could be identified by the presence of indentations of irregular outline at the tip of the endosperm and strands of the partly digested nucellar tissue which formerly had surrounded the antipodals (pl. 2, *A*). A partial or complete disappearance or resorption of the antipodal tissue at this period was noted in somewhat less than half of the ovules examined. In the remainder, the surviving antipodals in some cases exhibited little or no evidence of renewed growth activity; in others, active growth was in progress. An example of the former is shown in plate 2, *B*, the antipodals here being organized in a small spherical group of cells. Similar groups in later stages of kernel development are shown in plate 2, *C* and *D*. The persistence of these essentially unaltered groups of antipodal cells in relatively advanced stages of kernel development may be interpreted as evidence that growth activity is not the determining factor in the survival or disappearance of the antipodals in the ontogeny of the caryopsis.

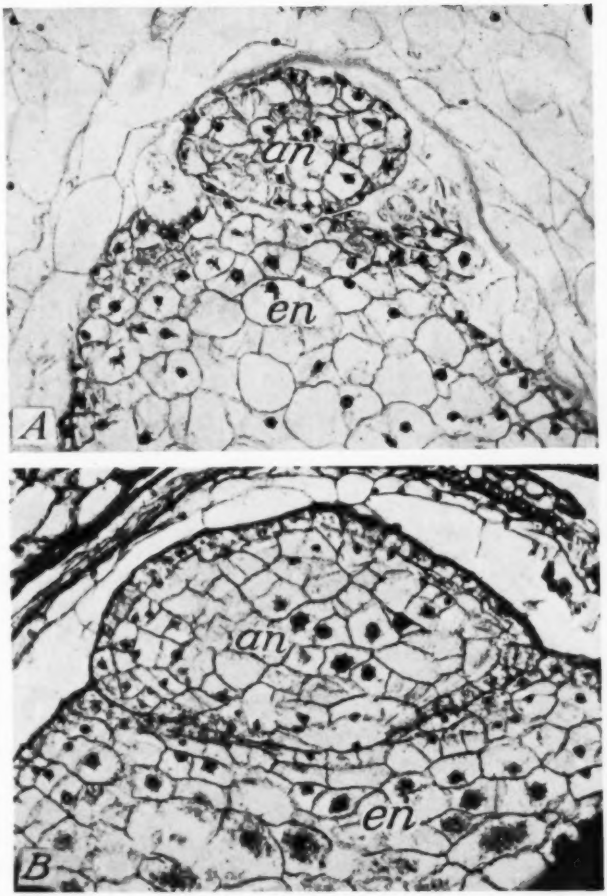
Initial stages of renewed growth activity of certain antipodal groups following the period of little or no growth immediately after fertilization were noted in young caryopses examined from 8 to 12 days after pollination. These early growth stages were characterized by an increase in the number and size of the cells without any apparent morphological differentiation within the antipodal tissue (pl. 3, *A*). In later developmental stages larger antipodal groups were noted in which there was a well-defined epidermis, a fairly definite arrangement of the subepidermal cells in radial rows, and within the innermost cells an accumulation of starch about the nuclei (pl. 3, *B*). With respect to the differentiation of an epidermis and the deposition of starch the antipodal tissue closely resembled the adjacent endosperm tissue in these stages; but with respect to cell size and nuclear size there was a noticeable difference, the cells and nuclei of the antipodal tissue being in general smaller than those of comparable regions in the endosperm. Presumably this size difference was due to the monoploid chromosome



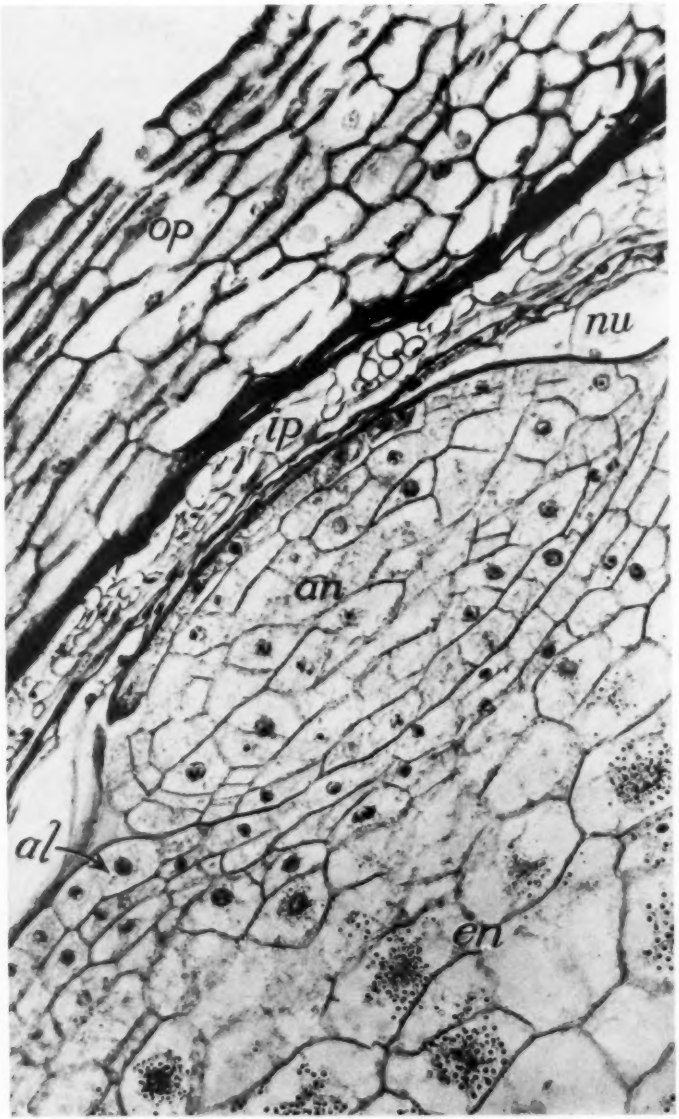
Antipodal tissue in early stages of kernel development; radial longitudinal sections: *A*, At time of fertilization; *B*, 4 days after pollination; *C* and *D*, 6 and 8 days after pollination, showing partial and advanced disintegration of antipodals. *an*, Antipodal tissue; *en*, endosperm; *es*, embryo sac; *nu*, nucellus. *A* and *B*, × 250; *C* and *D*, × 120.



Antipodal tissue: *A*, Disintegration essentially completed, 11 days after pollination; *B–D*, persistence of antipodals as small groups of undifferentiated cells, 12, 23, and 26 days after pollination. *an*, Antipodal tissue; *en*, endosperm. *A*, × 120; *B–D*, × 200.



Actively developing antipodal groups: *A*, At 11 days after pollination, with as yet no apparent orderly arrangement or differentiation of the antipodal tissue; *B*, at 22 days after pollination, showing a well-defined epidermis and evidence of internal differentiation. *an*, Antipodal tissue; *en*, endosperm. × 160.



An antipodal group and surrounding tissues of a young caryopsis 20 days after pollination, highly magnified to show cellular differentiation. Epidermis of the antipodal tissue and the epidermis or aleurone layer of the endosperm sharply delimited: *an*, Antipodal tissue; *en*, endosperm; *al*, aleurone; *nu*, nucellus; *ip*, inner pericarp; *op*, outer pericarp. × 300.

constitution of the antipodal tissue and the triploid constitution of the endosperm, since there is ordinarily a definite correlation between nuclear and cell size and number of chromosome sets.

Antipodal groups in intermediate stages of development were noted in which no reserve starch was present, although starch grains were present in abundance in the adjacent endosperm tissue (pl. 4). These groups not infrequently were as fully differentiated as were those of the same age in which starch was being deposited.

The antipodal tissue occupies a position in the crown region of the kernel during the more advanced stages of kernel development (pl. 5, *A*). During early ontogenetic development there was a progressive movement of the antipodals away from the micropylar region of the nucellus, where they were located in the initial stages of kernel development, toward the apical or crown region, this movement taking place as the endosperm enlarged and expanded into the region formerly occupied by the nucellus. During this translocation the antipodals retained the same relative position with respect to the endosperm, i. e., they remained at or near the crest of the expanding region farthest removed from the embryo.

At the 16-day stage of development (pl. 5, *A*) a very limited portion of the nucellus remained between the antipodal tissue and the ovary wall or pericarp. Integument tissue was visible only at the stylar-canal region, and cellular disintegration had commenced in the internal region of the pericarp in the subcrown region on both the abgerminal and the germinal face of the caryopsis. At the 20-day stage (pl. 4) the antipodal group was in direct contact with the inner pericarp except for an intervening noncellular remnant of the nucellus. The outer and inner regions of the pericarp were separated by a crushed layer of disintegrating cells.

Although the nucellus disintegrates almost completely and the pericarp is compressed and the constituent cells are much flattened as maturity approaches, there was no evidence of a similar compression or disintegration of the antipodals during the same stages.

Growth of the antipodal tissue in many instances persisted until the caryopsis approached morphological maturity. A large, essentially mature antipodal group, consisting of hundreds of cells closely packed with starch and completely surrounded by a fully differentiated epidermis without reserve starch, is shown in plate 5, *B*. The relative positions of the antipodal tissue, the endosperm, and the pericarp are shown in plate 5, *B*. This antipodal group, as well as the group shown in plate 4, was located in the subcrown region of the abgerminal face of the caryopsis rather than directly beneath the silk-attachment region at the crown of the kernel as in plate 5, *A* (cf. pl. 11, *B*). A more highly magnified portion of the antipodal group shown in plate 5, *B*, is reproduced at a slightly different focus in plate 5, *C*. This figure demonstrates the marked similarity in the cellular organization of the antipodal tissue and the tissue of the adjoining endosperm. Noteworthy is the marked resemblance between the epidermis of the antipodal tissue and the epidermis or aleurone layer of the endosperm. Neither of these epidermal layers contained starch grains, although the adjacent cells in both the endosperm and the antipodal tissue were filled with starch grains. Whether aleurone grains were present in the epidermis of the antipodal tissue as well as in the aleurone layer of the endosperm was not determined.

INTEGUMENTS

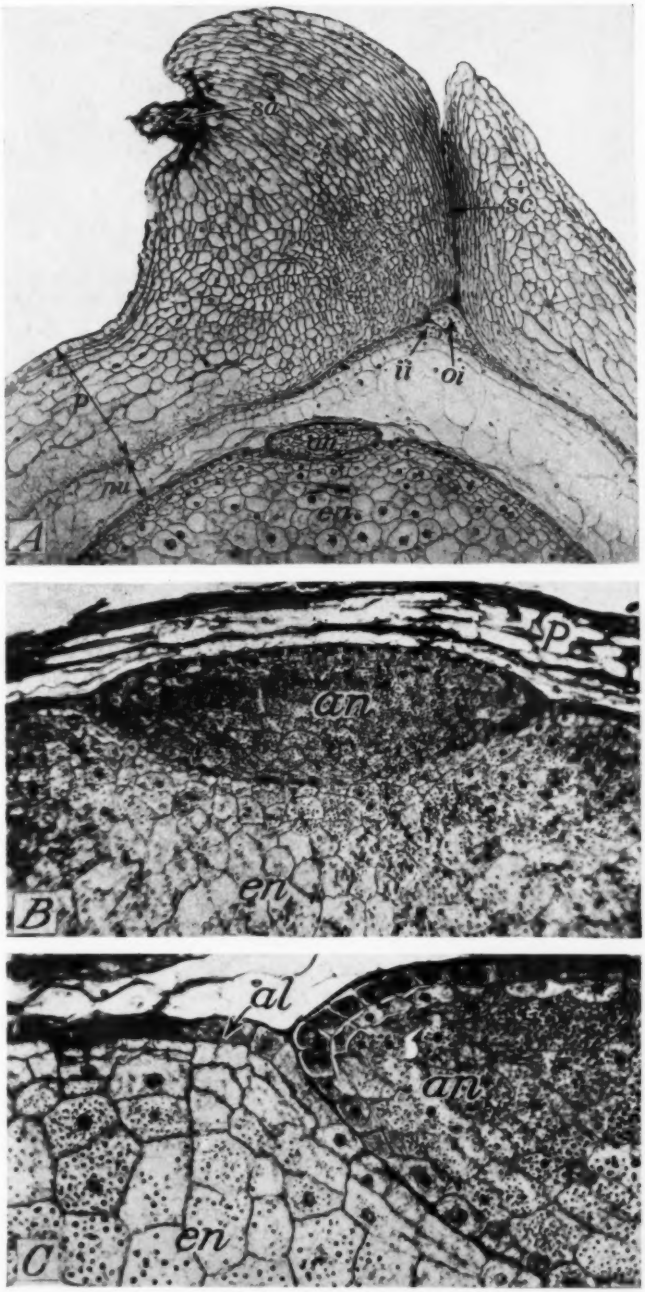
In many members of the grass family, especially the cereal grains, integument tissue persists in the mature caryopsis and forms a definite layer, the seed coat. Ordinarily it is the inner integument that persists, the outer integument disappearing as the kernel matures. There is no seed coat in the maize caryopsis, according to the observations of Guérin (*15*), Poindexter (*33*), Haddad (*19*), and others who have studied the developmental morphology of the maize caryopsis. Haddad observed a complete resorption of the integumental tissues in the hybrid between two inbred strains of sweet corn within 20 days after pollination, and a similar resorption occurred somewhat later in the parental inbred strains. However, True (*47*) and Weatherwax (*52*) stated that crushed remnants of integument tissue were present at maturity, and Weatherwax referred to this remnant as a testa. These conflicting reports suggest that different varieties of maize may differ appreciably in the extent to which the integuments are resorbed. But in no case has a typical seed coat consisting of a well-defined layer of integument tissue been reported in maize.

There is at present a conspicuous lack of uniformity in the use of the term "seed coat" as applied to the caryopsis of maize and other grasses. The pericarp has been called the seed coat by Weatherwax, and Artschwager has referred to the pericarp plus the integuments as the seed coat. Others have referred to the persistent nucellar and integument tissue as the seed coat. In physiological researches on the fruits of various members of the grass family, especially researches concerned with permeability, the terms "seed coat", "testa", and "seed coat membrane" often have been applied indiscriminately to the various portions of the external covering of the caryopsis, irrespective of their true morphological nature. According to long-established usage the term "seed coat" is properly applied only to the structure or structures present in the mature caryopsis which originated solely from integument tissue. When separate layers are formed by the two integuments the hard outer layer is called appropriately the "testa." As there seems to be no plausible reason for changing these definitions, the long-established usage of these terms is here retained. A careful developmental study of the integuments was made in order to determine whether or not a seed coat was present in the strains of maize under investigation.

The integuments of the mature ovule in *Zea* consist of thin-walled parenchyma cells. The inner integument is typically two cell layers in thickness except in the region of the micropyle, where there are from three to five layers. The outer integument has typically either two or three cell layers, but in the integument-insertion region and at the stylar-canal region there are from three to five or more layers of cells. Active growth of the integuments to keep pace with the increase in

EXPLANATORY LEGEND FOR PLATE 5

Antipodal tissue in kernels at various stages of maturity: *A*, Crown region of an immature caryopsis 16 days after pollination in radial longitudinal section at right angles to the germinal face, showing relative position of antipodal tissue. *B*, A morphologically mature antipodal group 43 days after pollination, packed with starch and surrounded by a well-defined epidermis closely resembling the aleurone layer or epidermis of the adjoining endosperm. Reproduced at a relatively low magnification to show the relative positions of the antipodal tissue, the endosperm, and the pericarp in the region of the caryopsis occupied by the antipodals. *C*, A portion of *B* more highly magnified to show cellular details more clearly. *aa*, Antipodals; *en*, endosperm; *al*, aleurone; *nu*, nucellus; *ii*, inner integument; *oi*, outer integument; *p*, pericarp; *sc*, stylar canal; *sa*, silk attachment region. *A*, × 25; *B*, × 80; *C*, × 200.



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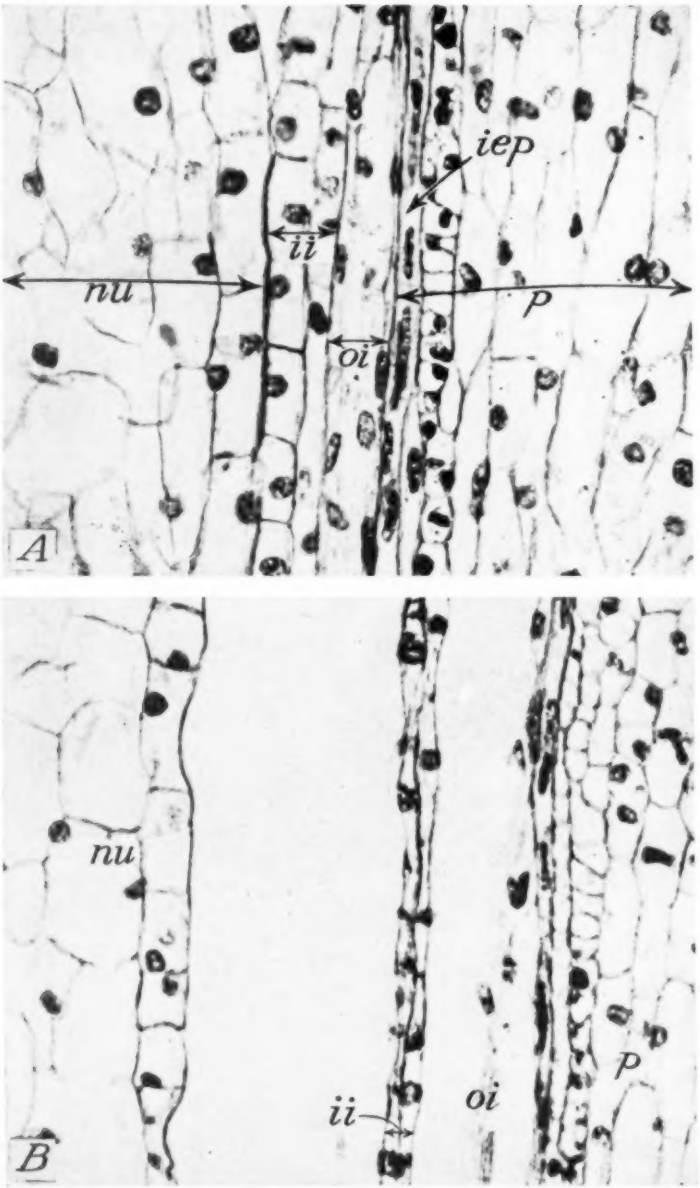


Integuments in the abgerminal region of a young caryopsis 7 days after pollination: *A*, Near the chalaza; *B*, In the subcrown region. Disintegration well advanced in outer but not in inner integument. Cell walls disappear first; later the cytoplasm and nuclei are resorbed. *ii*, Inner integument; *oi*, outer integument; *nu*, nucellus; *p*, pericarp; *iep*, inner epidermis of the pericarp. × 600.

the size of the ovule was in progress at the time of pollination and during the early embryonic stages. Cell-division figures were observed, especially in the basal regions of the integuments resulting in anticlinal wall formation. In later developmental stages, after disintegration of the integuments had begun, nuclear divisions continued even in regions where the cell walls had almost completely disappeared.

Initial stages in the disintegration of the integuments were noted in certain definitely localized regions in samples examined 3 days after pollination. These regions involved the inner integument over the germinal face of the young caryopsis and the outer integument over the abgerminal face at the chalazal region and in the subcrown region between the stylar canal and the base of the ovule. In 7-day samples (pl. 6, *B*) the break-down of the integuments in these regions was well advanced and was spreading rapidly into the other parts of the integuments. The illustrations of the integuments in plates 6 and 7 are photomicrographs of median radial longitudinal sections cut at right angles to the germinal face of the kernel.

The order of disappearance of the cell constituents of the integuments followed a regular sequence. First the walls of the cells disappeared (pl. 6, *A*). Then the cytoplasm became much reduced in amount (*oi*, pl. 6, *B*). Finally the nuclei of the cells associated with scattered remnants of cytoplasm were all that remained (pl. 7, *B*), and these subsequently disappeared more or less completely. The cell nuclei often remained for many days after the cell walls had entirely disappeared.

Although the inner integument began to disintegrate very early over the germinal face of the kernel, a similar disintegration of the inner integument over the abgerminal face did not take place until the outer integument in this region was in an advanced stage of disintegration (pl. 6, *B*). In the outer integument the break-down of the tissue occurred simultaneously in both the inner and outer cell layers (pl. 6), but the outer of the two cell layers of the inner integument regularly disappeared in advance of the inner layer of cells (pl. 7, *A*).

The inner integument was in an advanced stage of disintegration over the germinal face of the kernel 35 days after pollination. Occasional isolated nuclei were present between the inner epidermis of the pericarp and the outer wall of the nucellar epidermis (pl. 7, *C*), but elsewhere between these two layers at this same stage of kernel development, as illustrated in the lower part of this same figure (*C*), (*D*) there was no remaining trace of the inner integument tissue.

A complete disappearance of both integuments over most of the abgerminal face of the nearly mature kernels was the typical condition in specimens examined approximately 40 days after pollination (pl. 7, *D*). In the particular region of the kernel from which this photograph was taken there was no trace of any remnant either of integument tissue between the suberized nucellar membrane and the pericarp or of nucellar tissue between the aleurone and the nucellar membrane. However, in other regions of this preparation and in other specimens of the same and later stages of maturity an integument remnant in the form of flattened nuclei embedded in strands of cytoplasm occasionally could be identified. But no appreciable amount of

integument tissue in the form of a continuous covering about the kernel was present in the mature caryopsis.

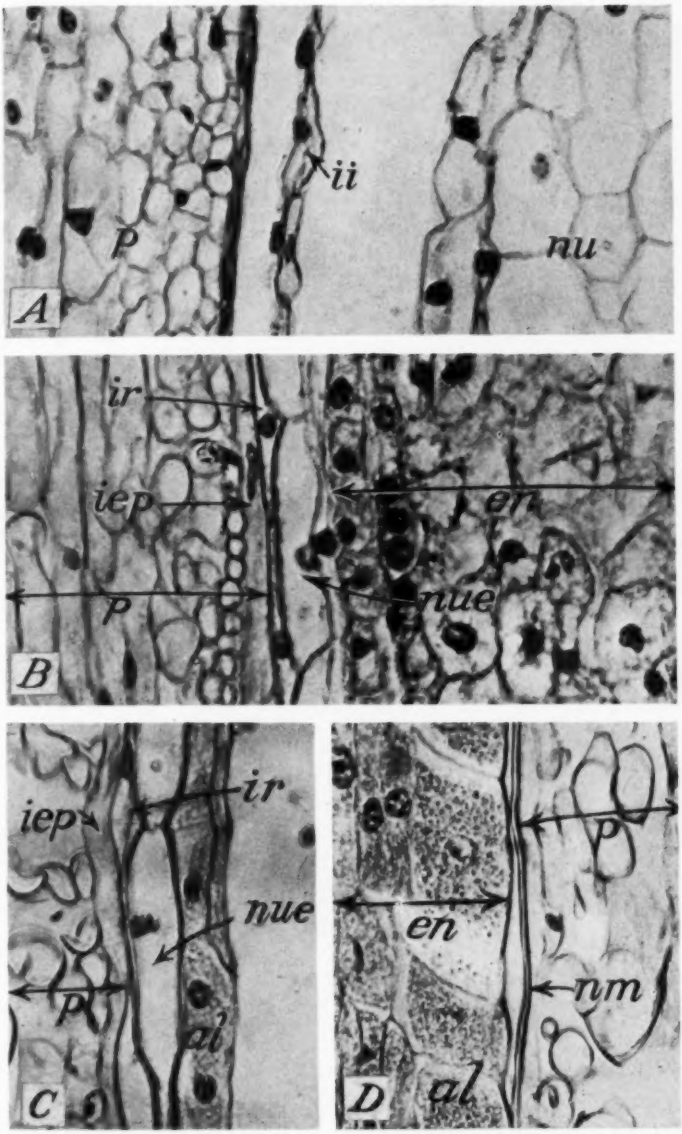
On the basis of this study of the history of the integuments during kernel development, a study which involved the examination of a very complete ontogenetic series of stages from the commercial variety Pride of Michigan, as well as a survey of a limited number of other stocks of maize, it was concluded that the maize caryopsis has no true seed coat. No appreciable amount of integument tissue was present at maturity. Scattered remnants representing the cell contents of integument tissue which had not been completely resorbed were noted in certain regions of some samples, but this remnant did not comprise a continuous layer or covering which properly could be referred to as a seed coat. In the mature caryopsis the suberized nucellar membrane was the only structure of constant morphological value present between the aleurone layer and the pericarp.

NUCELLAR MEMBRANE

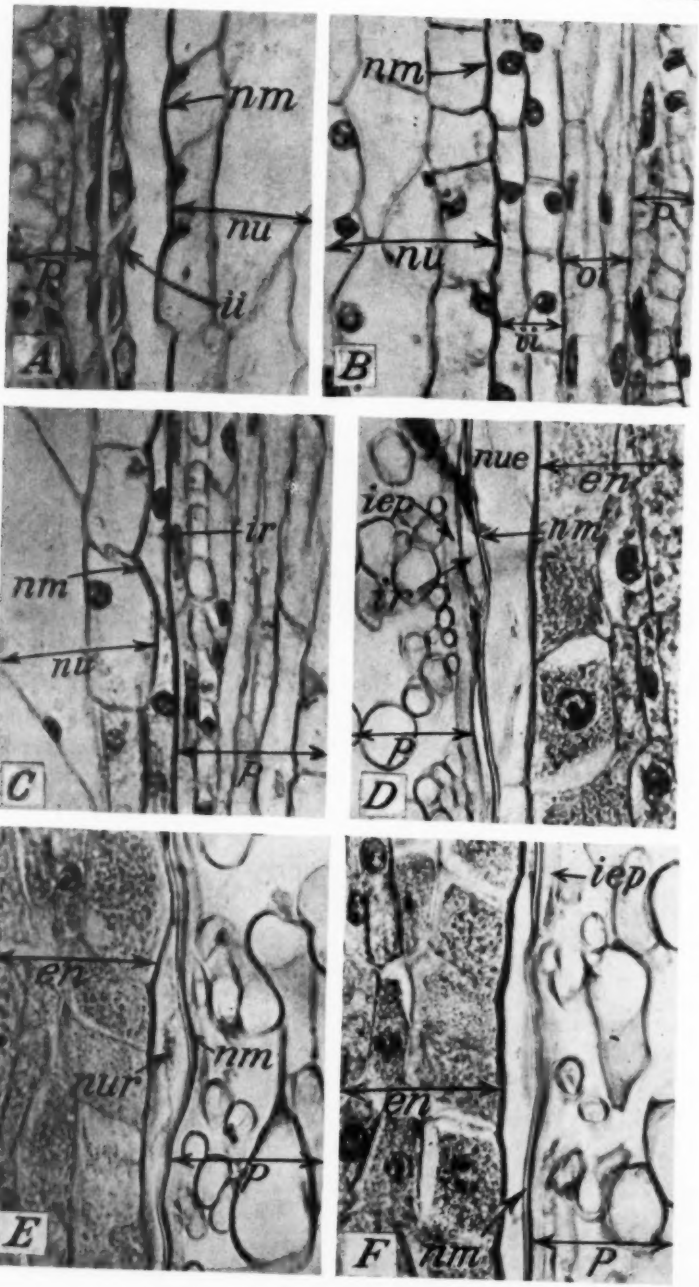
During the intermediate period in the development of the kernel, the nucellar membrane of the mature caryopsis differentiates as a suberized thickening of the outer cell walls of the epidermis of the nucellus. At the time of fertilization and during the initial stages in kernel development, the cells comprising this epidermal tissue had relatively thin walls, and tests with Sudan III and Sudan IV indicated that the walls were not suberized in these early stages. During the period from 6 to 10 days after pollination, the outer walls of the cells of the nucellar epidermis increased in thickness and became suberized (pls. 6, *B*; 7, *A*), first in the region adjacent to the chalaza (pl. 8, *A*, *B*) and later over the entire epidermis. The photomicrographs showing the development of the nucellar membrane were obtained from median longitudinal sections cut at right angles to the germinal face of the kernel. At 16 to 18 days following pollination, a definite suberized layer appreciably thicker than the original wall was present as an integral part of the nucellar epidermis (pl. 8, *C*, *D*). Soon thereafter the developing endosperm, which had already digested the inner region of the nucellus, encroached upon and destroyed the cellular organization of the outer portion of the nucellus, including the epidermis; only the suberized outer wall was left intact (pl. 8, *E*, *F*).

As these changes are taking place in the nucellus, the integuments are being resorbed. As stated previously, the cell walls of the integument tissue disappear first, the nuclei and cytoplasm of the cells often persisting for some time after the walls of the cells have vanished. Disintegration of both integuments is well advanced before the nucellar epidermis becomes extensively suberized (pl. 8, *C*, *D*). This relatively early and virtually complete disappearance of the integuments in maize is strikingly different from the situation in many other grasses in which integument tissue persists and forms the seed coat of the mature caryopsis.

The nucellus is represented in the mature caryopsis only by this suberized membrane and by discontinuous noncellular remnants of nucellar tissue between this layer and the aleurone (pl. 9). As previously stated, no true seed coat derived from integument tissue was observed in the mature caryopsis. The suberized nucellar membrane and the pericarp constituted the sole coverings of the maize kernel.



Stages in the disappearance of the integuments in germinal (*A–C*) and abgerminal (*D*) regions of immature caryopses: *A*, 7 days; *B*, 18 days; *C*, 35 days; and *D*, 40 days after pollination. In *A* the cell walls have disappeared in the outer of the two cell layers of the inner integument, the inner layer of cells being essentially intact. In *B* the integument remnant consists of disintegrating free nuclei and traces of cytoplasm lying between the inner epidermis of the pericarp and the nucellar epidermis. *C* shows a similar but more discontinuous remnant at a later stage. In *D* no integument tissue remains, consequently the nucellar membrane is directly in contact with the pericarp. *al*, Aleurone; *en*, endosperm; *iep*, inner epidermis of the pericarp; *ii*, inner integument; *ir*, integument remnant; *nm*, nucellar membrane; *nu*, nucellus; *nue*, nucellar epidermis; *p*, pericarp. × 600.



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The suberized nucellar membrane probably was observed by at least two of the early investigators of kernel morphology in maize. True (*47, p. 220*) mentioned the presence of a conspicuous "cuticle" associated with the nucellar epidermis of the ripe grain in *Zea*. Guérin (*15, p. 7*), after describing the disappearance of the integuments in maize during ontogenetic development, stated that at maturity "L'épiderme du nucelle a de même complètement disparu"; but he also referred to a seed coat represented only by "une bande comprimée dans laquelle il est impossible de retrouver la moindre structure cellulaire."

Brown (*5, 6*) was the first to demonstrate the semipermeable nature of the seed coat in a member of the grass family. Later, in certain cereals and other members of the Gramineae, Harrington and Crocker (*20*), Andersen (*1*), Gurewitsch (*17*), Tharp,[16] and Krauss (*24*) described a suberized semipermeable membrane associated with the integuments rather than with the nucellus, as in *Zea*. In *Zea*, the physiological researches of Shull and Shull (*40*), Orton (*32*), Beeskow,[17] and Tharp [16] demonstrated that the protective covering of the embryo and endosperm exhibits semipermeable properties. Beeskow attributed these properties to a layer, chiefly fatty or lipoid in character, formed by the disintegrating integuments. But it is more probable that the semipermeability of the maize caryopsis is due primarily to the presence of a suberized membrane of nucellar origin, an interpretation that has already been applied to the related forms having similar membranes, derived apparently from integument tissue.

PERICARP

The transformation of the ovary wall into the pericarp in *Zea* is a gradual process and requires the entire period from fertilization to maturity for its completion. A progressive series of changes is involved, which includes growth by cell division and cell enlargement, disintegration and collapse of cells in certain regions, extensive lignification of cell walls, and a final compression of the entire tissue into the relatively thin protective covering of the mature caryopsis. The amount of growth involved is very appreciable, since the dimensions of the mature kernel are from 8 to 12 times as great as those of the mature ovary from which it is derived. The following account of the development of the pericarp is essentially in agreement with the previous researches of True (*47*), Guérin (*15*), Randolph (*34*), and Haddad (*19*), which have provided a fairly complete description of the essential features of the process.

The ovary wall, which differentiates into the pericarp as kernel development proceeds, consists chiefly of thin-walled, undifferentiated

[16] THARP, W. H., JR. See footnote 6.
[17] BEESKOW, H. C. See footnote 5.

EXPLANATORY LEGEND FOR PLATE 8

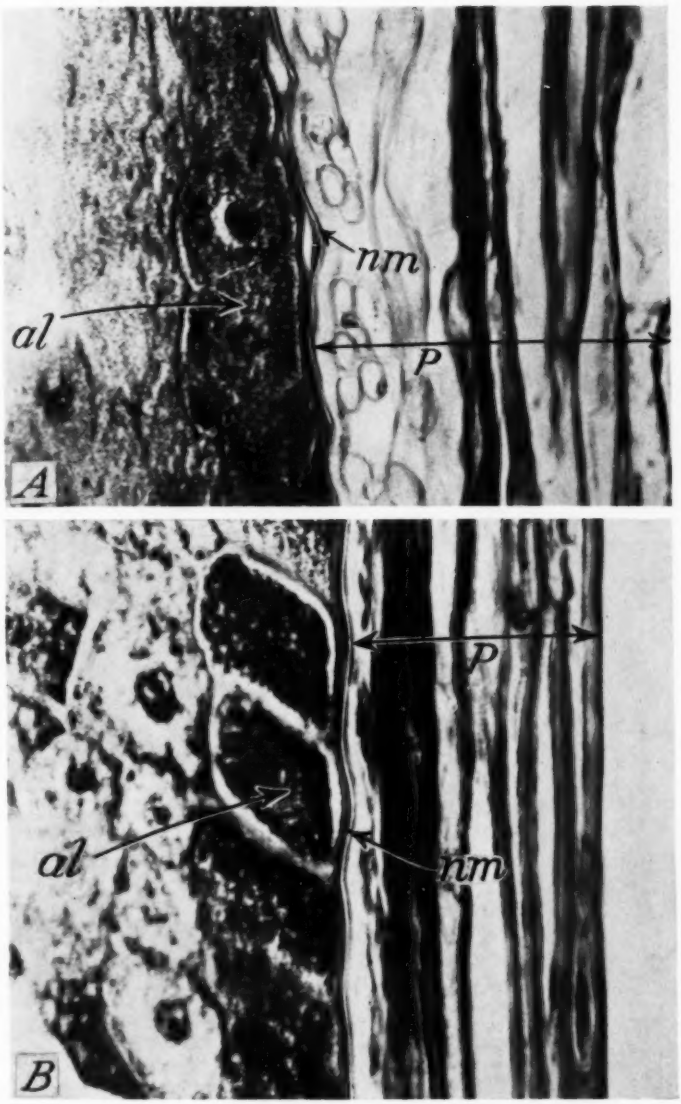
Various stages in the development of the nucellar membrane: *A*, Germinal region at 10 days, and *B*, abgerminal region at 6 days after pollination, showing the initial stages in the suberization of the nucellar epidermis in the region of the chalaza; *C*, abgerminal region at 18 days, showing an increased amount of suberization of the nucellar epidermis, the individual cells of the epidermis being still intact; *D*, germinal face at 23 days, showing an advanced stage in the resorption of the entire nucellus except the suberized outer cell walls of the nucellar epidermis which persist as the nucellar membrane; *E* and *F*, from the germinal face of kernels at 30 and 35 days, showing the nucellar membrane between the endosperm and the pericarp, with a noncellular remnant of nucellar tissue persisting between the endosperm and the membrane in *E*. *en*, Endosperm; *iep*, inner epidermis of the pericarp; *ii*, Inner integument; *ir*, integument remnant; *nm*, nucellus membrane; *nu*, nucellus; *nue*, nucellar epidermis; *nur*, nucellar remnant; *oi*, outer integument; *p*, pericarp. × 600.

parenchyma cells at the time of fertilization. There were many cell-division figures in the ovary-wall tissue, especially near the base of the ovary, in the initial stages of kernel development. Adjoining the inner region of the ovary wall, numerous small, isodiametric cells were being formed by a subdivision of the larger cells in this region. This growth activity began soon after fertilization and continued for 10 to 14 days (pl. 10). Elsewhere scattered division figures also were noted less frequently. These observations on early cell-division activity in the differentiating pericarp are not in agreement with the statement of Haddad (*19*) that the increase in the size of the ovary wall following the 1-day stage was accomplished by an increase in cell size rather than by an increase in the number of cells. An increase both in the number and in the size of the cells apparently contributed to the growth of the pericarp tissue.

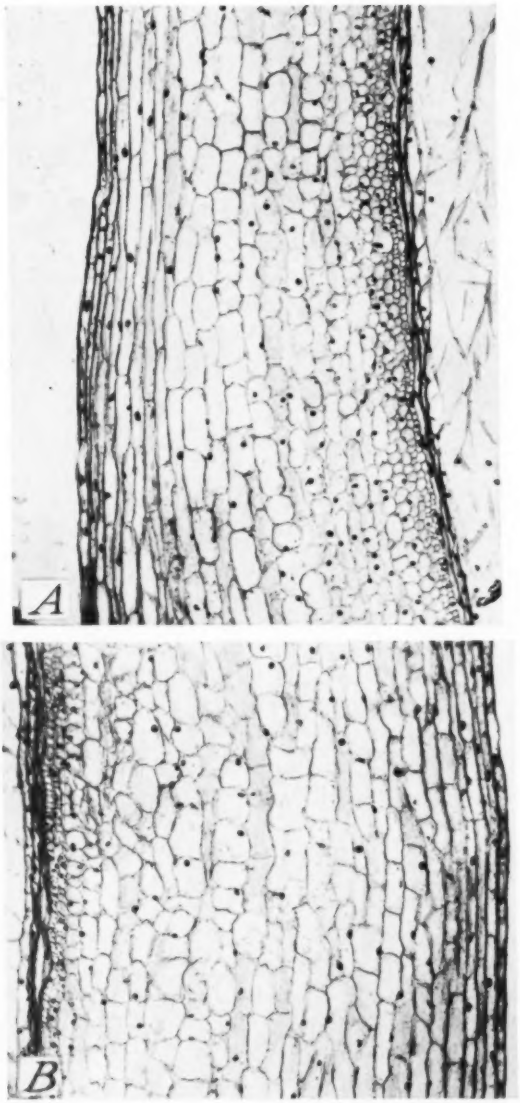
Within 10 days after pollination the ovary wall, or pericarp, had increased to approximately three times its original length and twice its original diameter. This increase was accomplished chiefly by an enlargement of the cells in the outer region and by both cell division and cell enlargement in the inner region (pl. 10). At about the 10-day stage the cells that were approximately halfway between the outer and inner limits of the pericarp in the subcrown region surrounding the base of the style began to disintegrate (pl. 11, *A*) and later became crushed together, forming a thin layer of noncellular material (pl. 11, *B*). At 10 to 14 days the inner epidermis consisted of cells which in the radial longitudinal sections appeared very much elongated and narrow (cf. pls. 7, *D*, and 8, *B*); in transverse sections they were small and nearly circular in outline. There were frequently one to three or more additional layers of cells of this type adjoining the inner epidermal layer. Just beneath these cells there were a few layers of cells rather similar to the epidermal cells but with their long axes at right angles to those of the epidermis; thus, these deeper lying cells appeared as elongated cells in the cross sections and as small circular cells in the longitudinal sections (pl. 7, *B*).

The pericarp increased in thickness up to 9 to 12 days in the crown region and up to 15 to 18 days in the basal region. This difference in the time at which different parts of the pericarp attained a maximum thickness was due primarily to the fact that the disintegration of the middle portion of the pericarp took place at the crown region earlier than in the basal region. Thereafter a cessation of lateral growth activity, accompanied by disintegration in the middle region and compression of the tissue laterally, resulted in a gradual decrease in the thickness of the pericarp in the later stages of maturity. However, elongation of the pericarp from the base of the kernel to the crown region and increase in circumference continued until the kernel was morphologically mature and the embryo and endosperm ceased to expand.

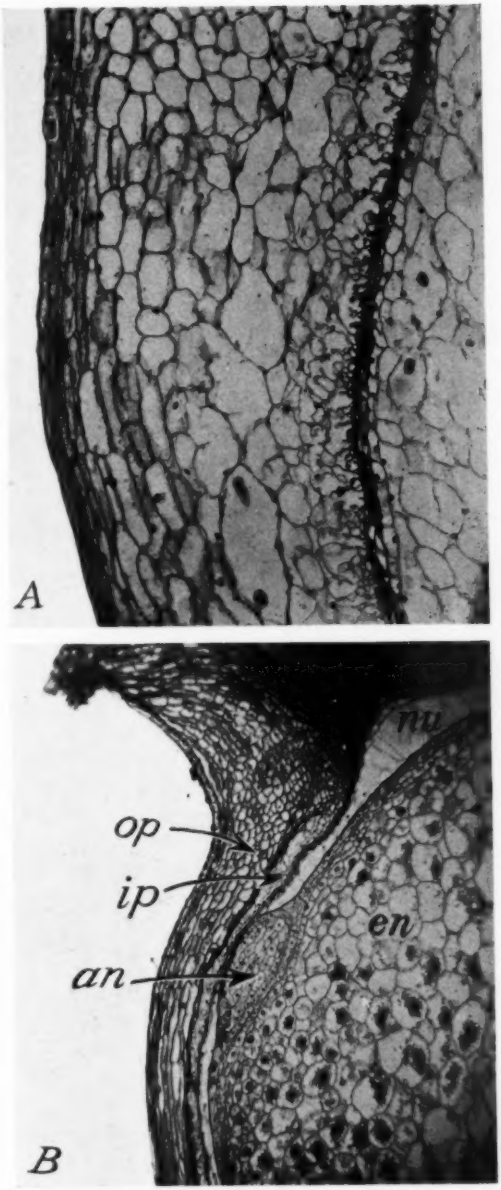
The disintegration and partial resorption of the cells in the central portion of the subcrown region of the pericarp (pl. 11, *A*) were followed by a collapse and compression of the tissue in this region, leaving a layer of noncellular material separating the outer and inner regions of the pericarp (*B*). This partial disintegration and collapse of cells in the middle region of the pericarp, which began first in the subcrown region, gradually extended toward the base of the kernel and thus delimited the inner and outer pericarp over the entire surface of



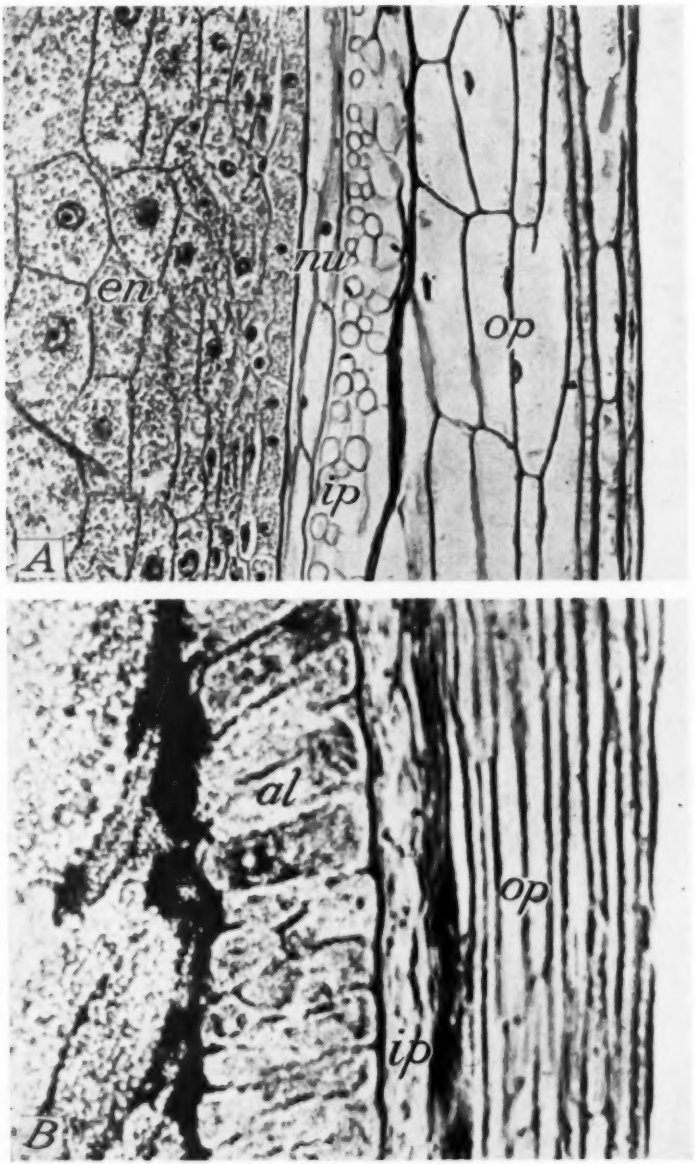
Sections from the abgerminal face of nearly mature kernels in the region of the nucellar membrane: *A*, 40 days after pollination; *B*, 48 days after pollination. In *A* the nucellar membrane is in contact with the inner epidermis of the pericarp, but there is a narrow space between the membrane and the aleurone which is partly filled with disorganized nucellar tissue. In *B* the nucellar membrane appears as a narrow band of uniform width between the aleurone layer and the inner margin of the pericarp. *nm*, Nucellar membrane; *al*, aleurone layer; *p*, pericarp. × 600.



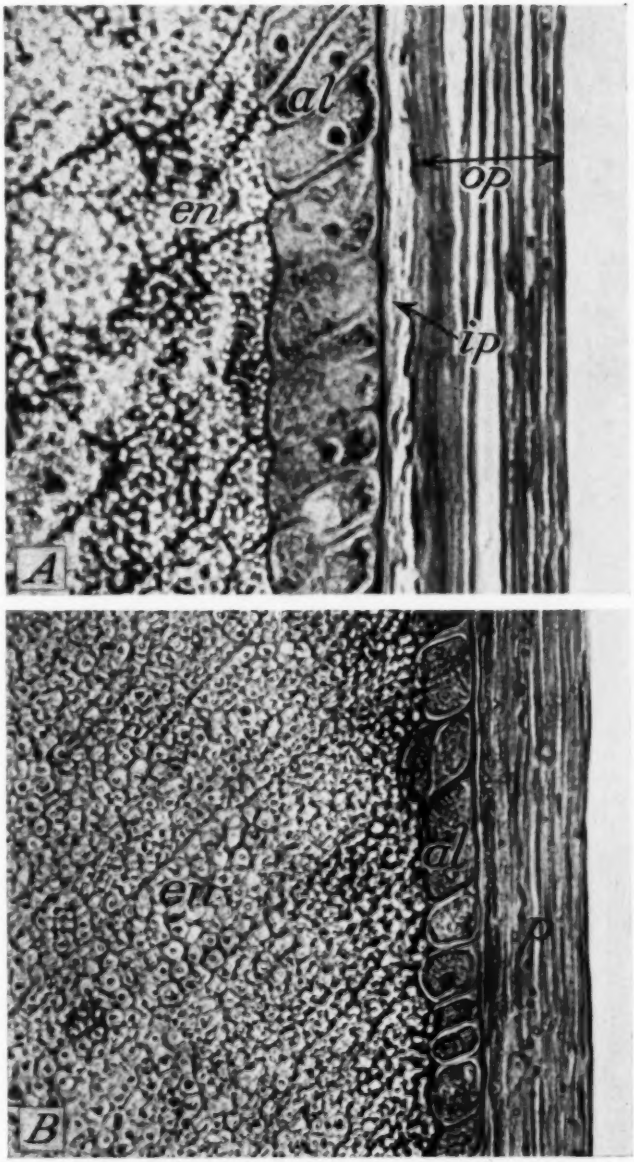
Median longitudinal sections of the pericarp of young kernels 10 days after pollination, the sections being taken at right angles to the germinal face of the kernel: *A*, Germinal face; *B*, abgerminal face midway between the tip and the base of the kernel. × 125.



The pericarp in the subcrown region over the germinal face of developing kernels: *A*, Highly magnified to show clearly the initial stages of cellular disintegration in the middle region of the pericarp 10 days after pollination; *B*, a lower magnification showing a more extensive portion of the subcrown region 20 days after pollination. *op*, Outer pericarp; *ip*, inner pericarp; *an*, antipodal tissue; *nu*, nucellus; *en*, endosperm. *A*, × 160; *B*, × 60.



Longitudinal sections of pericarp and adjacent tissues in midabgerminal region of developing kernels: *A*, 23 days after pollination; *B*, 40 days after pollination. *ip*, Inner pericarp; *op*, outer pericarp; *nu*, nucellus; *al*, aleurone; *en*, endosperm. × 250.



Longitudinal sections of pericarp and adjacent tissues in midabgerminal region of nearly mature (*A*) and mature (*B*) kernels: *ip*, Inner pericarp; *op*, outer pericarp; *p*, pericarp; *al*, aleurone; *en*, endosperm. *A*, × 250; *B*, × 160.

the kernel, except in the silk-attachment region and in the basal attachment region of the kernel. The basipetal succession of this process of tissue differentiation was in general characteristic of the order of development in the pericarp throughout its ontogenetic history.

The cells of the outer pericarp increased materially in size and gradually developed relatively thick walls with numerous simple pits during the period from 20 to 40 days after pollination (pl. 12). Intercellular spaces were lacking in the outer region; the cells remained intact and did not become separated from one another as development proceeded. A strikingly different type of behavior characterized the cells of the inner pericarp during this period. Here the cells remained thin-walled and, failing to increase in size as the expansion of the pericarp progressed, they became widely separated from one another (pl. 12, *A*). During the same period, however, the cells of the inner epidermis of the pericarp elongated very appreciably and to a sufficient extent to maintain the continuity of the epidermis as a well-defined layer of cells (pl. 7, *B*, *C*). Thus the epidermal cells were long and narrow viewed in longitudinal sections at right angles to the germinal face of the kernel, but in cross sections they were nearly circular. Eventually, as the kernel continued to enlarge in circumference these inner epidermal cells were drawn apart laterally and presented the appearance of a network, the so-called "cellules tubulaires" of Guérin, over the inner face of the pericarp.

The final stages of pericarp development were characterized by a continued increase in the thickness of the cell walls, especially the tangential walls, of the outer pericarp and by a gradual compression laterally of the entire pericarp (pls. 12, 13). Plate 12, *A* and *B*, and plate 13, *A*, may be compared directly, since they are reproduced at the same magnification, but plate 13, *B*, is reproduced at a somewhat lower magnification. As maturity approached the inner pericarp became more and more compressed until it was scarcely distinguishable as a separate region (pl. 12, *A* and *B*), except near the base of the kernel where it remained separate. The lumina of the cells in the outer pericarp gradually disappeared, owing to lateral compression and increase in wall thickness. In the mature pericarp (pl. 13, *B*) the much thickened and extensively lignified tangential walls of the individual cells were closely appressed and formed a firm protective covering for the caryopsis.

SUMMARY AND CONCLUSIONS

The morphology of the pistillate spikelet, the ovary, and the ovule in maize (*Zea mays* L.), is described briefly, and this description is followed by a detailed account of the developmental history of the caryopsis, together with a consideration of the time factor, temperature, and seasonal variations in relation to pollen-tube growth, fertilization, and kernel development.

Pollination is followed by germination of the pollen and establishment of the pollen tube in the stigmatic hairs of the silk within 5 to 10 minutes under ordinary conditions of temperature and humidity. Active protoplasmic streaming accompanies the early growth stages of the pollen tube. During the period from 2 to 4 hours after pollination the male nuclei migrate from the pollen grain into the pollen tube

through the actively streaming protoplasm and begin their passage to the embryo sac.

The time interval from pollination to fertilization under field conditions in which the maximum day temperatures ranged from 25° to 30° C. and the minimum night temperatures ranged from 13° to 17° was approximately 16 hours for silk lengths of 3 to 5 cm and 23 hours for silk lengths of 15 to 18 cm.

The primary endosperm nucleus divides within 2 to 4 hours after fertilization, and four to eight endosperm nuclei are formed at the time the zygote divides to form the two-celled proembryo at 10 to 12 hours after fertilization.

The major morphological changes in the transformation of the pistil into the mature caryopsis involve (1) the complete displacement of the ovule and integument tissues by the embryo and endosperm, (2) the formation of a suberized membrane derived from the epidermis of the nucellus, and (3) the transformation of the ovary wall into the pericarp. These changes were traced in a close series of stages obtained from material fixed at definite intervals following controlled pollinations.

The proembryo develops very irregularly in the initial stages, with no very orderly arrangement of cells or sequence of cell divisions. It conforms with the classical descriptions of grass embryos only to the extent that regular tiers of three or four cells with parallel cross walls occasionally are formed; but this type of proembryo is only one of a diverse series, the members of which differ markedly in the manner in which wall formation takes place.

The sectors of the proembryo in the initial stages of development are rapidly obscured as growth continues, being virtually obliterated well in advance of the delimitation of the plumule-radicle axis of the mature embryo. This early disappearance of the first cleavage planes and the variation in their relative positions in different embryos make it impossible to determine or to predict with reasonable accuracy which sector or sectors give rise to the root and shoot regions of the plumule-radicle axis.

The epidermis is differentiated as a separate tissue, first over the apical region of the proembryo and somewhat later elsewhere, during the period from 7 to 10 days after pollination.

The axis of the more mature embryo may be recognized 9 or 10 days after pollination as a group of meristematic cells in the anterior portion of the embryo. This permanent plumule-radicle axis is a lateral structure oriented in an oblique position with reference to the axis of the proembryo. At maturity the plumule-radicle axis assumes a position essentially parallel to that of the scutellum, by which it is almost completely surrounded.

The major portion of the proembryo, which does not contribute to the main axis of the embryo proper, continues to enlarge and becomes the massive scutellum of the mature embryo.

The basal suspensor region of the proembryo ceases growth soon after the plumule-radicle axis forms and persists merely as a vestigial organ at the base of the more mature embryo.

The coleoptile arises as the first ridge of tissue which develops first above and later around the stem meristem. The first seedling leaf arises next as a second ridge of tissue identical with but opposite that which gives rise to the coleoptile. Later three to five additional seed-

ling leaves make their appearance, as the embryo matures, in positions alternating with those of the coleoptile and the first seedling leaf.

The primary seedling radicle is differentiated within the internal region of the proembryo above the suspensor; as the cells of this region multiply they assume orderly arrangements and thus delimit the epidermal tissue and underlying portions of the radicle primordium. The tissue of the proembryo surrounding the young radicle develops as an ensheathing structure, the coleorhiza.

The limited scope of the investigation precluded a consideration of the homologies of the scutellum, the coleoptile, the coleorhiza, and other organs of the embryo.

The endosperm in its early development passes through the usual free-nucleate stage and becomes cellular approximately 4 days after pollination. At first, cell-division activity is prevalent throughout the endosperm; later it becomes localized in the peripheral region with periclinal wall formation taking place repeatedly in the epidermal layer and somewhat less frequently in the subepidermal cells.

The epidermal layer of the endosperm ceases active periclinal wall formation approximately 20 to 22 days after pollination and subsequently becomes the aleurone layer. Cell-division activity persists in the subepidermal cells, particularly in the middle region between the base and the tip of the endosperm, until maturity is approached. The growth of the inner portion of the endosperm during most of the developmental period is by cell enlargement rather than by active cell division.

The antipodal cells often proliferate during kernel development and persist in the mature caryopsis as an oval-shaped mass of haploid tissue between the aleurone layer and the pericarp at the tip of the kernel.

The integuments of the ovule disintegrate and virtually disappear during the early development of the caryopsis. Scattered noncellular remnants of integument tissue in the form of a very thin discontinuous layer were occasionally noted in advanced stages of kernel development. A seed coat consisting of a well-defined layer of integument tissue is lacking in the varieties of maize examined during the course of this investigation.

A suberized nucellar membrane derived from the outer wall of the nucellar epidermis was present in the mature caryopsis as a continuous, well-defined layer between the aleurone and the pericarp.

The ovary wall is transformed into the pericarp of the kernel. The process involves cell multiplication and cell enlargement in the early stages, subsequent disintegration and collapse of the middle region, and an extensive thickening of the tangential walls of the cells in the outer region, which is followed by a compression of the entire tissue to form the tough protective covering of the mature caryopsis.

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RESISTANCE TO BACTERIAL WILT OF OPEN-POLLINATED VARIETIES OF SWEET, DENT, AND FLINT CORN [1]

By S. S. IVANOFF [2]

Research associate in plant pathology, Wisconsin Agricultural Experiment Station

INTRODUCTION

Studies have been made on resistance of approximately 120 open-pollinated varieties of sweet, dent, and flint corn (*Zea mays* L.) to bacterial wilt, caused by *Phytomonas stewarti* (Smith) Bergey et al.

The resistance of a number of open-pollinated varieties of sweet corn had been tested earlier through natural infection by Smith (*6*),[3] Thomas (*8*), Rand and Cash (*4*, *5*), and others, whose work has already been reviewed by Ivanoff and Riker (*2*). Stated briefly, their results showed that the later sweet corn varieties were as a rule more resistant than the earlier ones. So far no extensive reports have been published on the varietal resistance of dent and flint corn to bacterial wilt. The occasional inclusion of some of these corns in resistance trials has shown that the dent corn varieties appeared more resistant than the sweet and flint corn varieties.

Corn growers from the Midwestern and Eastern States, where the wilt disease has been particularly prevalent and where late field corns are ordinarily grown, have often observed that field corn varieties withstood the disease better than sweet corn varieties. The belief in the higher resistance qualities of field corn as such has prevailed among some corn breeders who have attempted to cross sweet corn with field corn in the hope that they might obtain an early sweet corn variety with the highly resistant qualities of field corn. The question whether the field corn varieties grown in the Middle West are highly resistant because of some type of resistance inherent in these varieties or because of their relatively great height and lateness arose soon after it was found that lateness and height were associated with the resistance of Golden Bantam sweet corn inbreds and crosses (*2*).

The purpose of these studies was threefold: (1) To evaluate each variety, particularly those of the sweet corn group, for resistance to the disease, with a view to aiding the corn grower in his selection of varieties for planting in localities where the disease is of economic importance; (2) to investigate correlations of resistance with other plant characters within each of the three varietal groups; and (3) to compare the resistance of the sweet corn varieties with that of dent and flint varieties. The results are presented without further repetitions because they seem to be entirely in accord with those on sweet corn conducted during three seasons (Ivanoff and Riker (*2*)).

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[2] The writer gratefully acknowledges his indebtedness to members of several State agricultural experiment stations and to a number of commercial firms for supplying seed, and to the California Packing Corporation (Midwest Division) for supplying land and labor for the work.

[3] Reference is made by number (italic) to Literature Cited, p. 925.

MATERIALS AND METHODS

The corn tested consisted of 92 open-pollinated sweet, 17 dent, and 11 flint corn varieties. Four dent corn hybrids were also included. The material was obtained from various sources, and was characterized by its diversity in respect to several important plant characters, particularly height and time of maturity. Thus among each of these three varietal types of corn there were some varieties which were very early, reaching edible ear stage in about 60 to 70 days, others which were medium early, and still others, such as Honey June, Leaming, and Kutias, which were very late. The difference in maturity between the earliest and latest corn was more than a month. The height of the various varieties ranged from 32 to 123 inches. The trials were conducted in northern Illinois during the summer of 1935.

The methods employed in these studies for planting, inoculating, and taking results were similar to those reported by Ivanoff and Riker (*2*) in the study of resistance to bacterial wilt of inbred strains and crosses of sweet corn. The more important of these methods, briefly stated, are as follows:

Each variety was represented by at least two rows of about 45 plants each. One of the rows was inoculated and the other left for control. Some varieties were replicated from 2 to 15 times.

The plants were artificially inoculated at the most susceptible stage by means of a plant inoculator which has been described by the writer (*1*). The method of artificial inoculation has been found not only to be adequate, but also to possess advantages over natural infection in disease-resistance studies.

A standardized suspension of five cultures of *Phytomonas stewarti* was used for the inoculations.

The height of the plants was measured at the time of maturity. The lateness of a corn variety was judged by the silking date, which was the date on which 75 percent of the corn plants came into silk. The records on height and lateness were taken on the uninoculated control rows.

The degree of resistance of each inoculated plant was estimated on the basis of degree of injury at the time of harvesting. Each plant was given one of the following five indexes of resistance: 0, 25, 50, 75, and 100. These indexes corresponded to five more or less distinct degrees of disease injury. A plant which at the time of record taking was found dead, with all of its parts dry and light brown in color on account of the disease, was very stunted, and had a very small ear or no ear at all, received an index of resistance of 0. A plant which appeared normal, like the control plants of the same strain (even though the bacteria were present within its tissue), received an index of resistance of 100. Between these two extreme degrees of reaction to the inoculations, there were plants which exhibited three other degrees of injury intermediate between the two just mentioned. These plants were given indexes of resistance of 25, 50, and 75. The index of resistance for an entire strain was estimated as the arithmetical mean of the indexes of all the plants of that strain. These indexes corresponded roughly to the percentage yield at the time of harvesting. In comparing the indexes of resistance of two varieties, a difference of a few points should not be considered significant. All corn was planted May 24.

EXPERIMENTAL RESULTS

Great differences in resistance were found among the varieties of each of the three varietal groups. Within each group there were some varieties which died from the disease sometime before harvesting for canning and produced no ears at all, while a few other varieties reached canning stage with very little loss in yield. The majority of the varieties, however, occupied a place between these two extreme limits. Alphabetical lists of all the sweet, dent, and flint corn varieties tested, with a measure of the maximum height, silking date, and index of resistance for each variety, are given in tables 1 and 2.

TABLE 1.—*Alphabetical list of open-pollinated sweet corn varieties inoculated with Phytomonas stewarti in 1935, with an indication of their maximum height, silking date, and index of resistance* [1]

Variety [2]	Color of kernel	Maximum height	Silking date	Index of resistance
		Inches		
Abbott and Cobb Early	White	78	Aug. 6	55
Alameda	do	68	Aug. 1	23
Alameda Sweet	do	67	do	27
Alpha	do	58	July 25	0
Aroostook	do	58	do	0
Banana Cream, Will's	do	81	July 29	11
Bantam Evergreen	Yellow	87	Aug. 8	56
Banting	do	32	July 22	0
Barden Wonder Bantam	do	70	July 31	25
Black Mexican	Black	71	Aug. 5	41
Burbank Bantam	Yellow	68	Aug. 4	30
Canada Gold	do	55	July 31	0
Carmel Golden	do	58	Aug. 2	8
Charlevois	do	64	Aug. 6	9
Colossal, Maule's	White	90	do	52
Columbia	do	55	Aug. 2	0
Country Gentleman	do	77	Aug. 14	74
Crosby	do	73	Aug. 4	7
Dorinny	Yellow	49	July 25	0
Earliest, Vaughan's	White	52	July 27	0
Early Columbia	do	69	Aug. 1	19
Early Dow	do	52	July 25	10
Early Evergreen	do	89	Aug. 12	69
Early Fortune	do	54	July 29	0
Early Golden Sweet	Yellow	41	do	0
Early June, Will's	White	46	do	0
Early Market	do	43	July 31	0
Early Minnesota	do	75	Aug. 8	39
Early Saskatchewan	do	51	July 29	5
Early Sunshine	Yellow	63	do	10
Early Surprise	White	52	Aug. 2	5
Early Sweet	do	71	do	14
Early White Cory	do	53	July 29	0
Early White Market	do	54	July 25	0
Early Yellow Sensation	Yellow	54	July 29	0
Extra Early Adams	White	80	Aug. 2	53
Extra Early Bantam, Harris'	Yellow	67	July 29	0
Extra Early Golden	do	47	Aug. 2	0
Extra Early Golden Bantam	do	66	July 31	5
First of All, Maule's	White	70	Aug. 2	45
Ford Early	do	60	do	15
Gold Coin	Yellow	74	Aug. 6	41
Golden Bantam	do	62	Aug. 2	15
Golden Cory	do	61	July 29	10
Golden Country Gentleman, Henderson's	do	69	Aug. 8	47
Golden Cream	do	65	Aug. 6	65
Golden Early Market	do	53	July 24	0
Golden Evergreen	do	92	Aug. 6	75
Golden Gem	do	50	July 25	0
Golden Gentleman	do	65	Aug. 10	42
Golden Giant	do	77	Aug. 2	46
Golden Giant, De Lue's	do	69	do	66
Golden Rod	do	80	do	40
Golden Sixty Day	do	53	July 25	25
Golden Sugar, Ford	do	78	Aug. 10	85
Golden Sunshine	do	65	July 29	23
Honey June	White	120	Aug. 18	95

[1] The garden varieties, or the Adams varieties, usually grown in the Southern States, have been included in these studies in the sweet corn group.

[2] The names of the varieties are those supplied by the cooperators and no grouping of synonyms has been made. For detailed descriptions of sweet corn varieties see Tapley, Enzie, and Van Eseltine (7).

TABLE 1.—*Alphabetical list of open-pollinated sweet corn varieties inoculated with Phytomonas stewarti in 1935, with an indication of their maximum height, silking date, and index of resistance*—Continued

Variety	Color of kernel	Maximum height	Silking date	Index of resistance
		Inches		
Howling Mob	White	76	Aug. 2	51
Imperial Mammoth	do	81	Aug. 8	64
Improved Golden Bantam, Gill's	Yellow	64	July 31	16
Kingcrost Canning Bantam	do	58	do	30
Kingcrost Golden Bantam	do	56	July 29	30
Lead All, Maule's	White	97		75
Long Island Beauty	do	96	Aug. 15	77
Mammoth Late	do	77	Aug. 14	73
Mammoth White Cory	do	38	Aug. 2	0
Maule XX	do	80	Aug. 6	60
Mayflower	do	69	Aug. 2	37
Money Maker	do	94	Aug. 12	85
Narrow Grained Evergreen	do	88	Aug. 15	70
Nectar	do	82	Aug. 12	70
Ne Plus Ultra	do	82	do	70
New Jersey Early White	do	73	Aug. 2	44
Nuetta	Yellow-red	60	July 27	0
Oregon Evergreen	White	80	Aug. 11	68
Pickaninny	Black	43	July 23	0
Portland Market	White	52	Aug. 2	0
Sixty-Day White	do	49	July 27	0
Spanish Gold	Yellow	55	do	0
Standard Bantam	do	59	Aug. 6	10
Stowell Evergreen	White	85	Aug. 12	69
Sunshine	Yellow	58	Aug. 1	8
Super Golden Sweet	do	83	Aug. 10	54
Surecropper Sugar	White	103	Aug. 16	90
Surprise	do	46	Aug. 2	0
Sweet Orange	Yellow	77	Aug. 8	32
Texas Evergreen	White	106	Aug. 16	75
Tucker Favorite	do	111	do	90
Whipple Early White	do	68	Aug. 6	32
Whipple Early Yellow	Yellow	76	Aug. 7	42
Whipple White	White	82	Aug. 2	70
Wood Southern Sweet Corn	Yellow	117	Aug. 16	80

TABLE 2.—*Alphabetical list of open-pollinated dent and flint corn varieties and crosses inoculated with Phytomonas stewarti, with a measure of their maximum height, silking date, and index of resistance*

Variety	Replications	Maximum iheght	Silking date	Index of resistance
Dent:	*Number*	*Inches*		
Extra Early Minnesota 13	2	76	Aug. 4	43
Extra Early Northwestern Dent	4	67	July 29	21
Extra Early Rustler White Dent	1	73	Aug. 8	47
Falconer Yellow Dent	1	68	July 31	19
Funk 176A	1	104	Aug. 16	85
Golden Glow	2	98	Aug. 12	73
Golden King Yellow Dent	3	95	Aug. 7	70
Iowa hybrid 931	1	107	Aug. 8	85
Iowa hybrid 939	1	108	do	85
Iowa hybrid 942	1	108	Aug. 10	85
Krug	1	123	Aug. 14	80
Leaming	3	113	do	80
Minnesota 13	2	94	Aug. 7	75
Murdock	3	102	Aug. 11	78
Northwestern Red Dent	1	79	Aug. 2	44
Rustler White Dent	1	90	Aug. 4	58
Silver King White Dent	1	102	Aug. 8	80
Wisconsin 7 Silver King	1	89	Aug. 12	75
Wisconsin 25 (Standard)	1	87	Aug. 2	9
Wisconsin 25 (Improved)	4	90	do	36
Wisconsin hybrid (A × Hy) × R_3	1	112	Aug. 10	85
Flint:				
Gehu North Dakota Yellow Flint	3	52	July 29	2
Kutias	3	107	Aug. 16+	85
Longfellow Yellow Flint	1	82	Aug. 8	40
Manitoba Flint	1	68	July 31	10
Mercer Yellow Flint	1	71	Aug. 2	23
Michigan Flint	1	51	July 29	0
North Dakota White Flint	1	56	do	6
Rainbow Flint	1	86	Aug. 4	21
Smutnose Flint	3	80	Aug. 2	15
Squaw Mixed Colored Flint	1	50	July 29	0
Triumph Yellow Flint	1	80	Aug. 2	30

The correlation between resistance and lateness of the corn (lateness indicated by the silking date), previously established for open-pollinated varieties of sweet corn by other investigators, already mentioned, was confirmed in these studies. The coefficient of simple correlation [4] between resistance and lateness estimated on the basis of the sweet corn varieties employed in these studies was $r=0.86\pm 0.018$. Similar correlation was also found among the dent and flint varieties (table 5).

TABLE 3.—*Correlations of both silking date and height with resistance to bacterial wilt of sweet, dent, and flint corn varieties*

Date of silking	Sweet corn			Dent corn [1]			Flint corn		
	Varieties	Average maximum height	Average index of resistance	Varieties	Average maximum height	Average index of resistance	Varieties	Average maximum height	Average index of resistance
	Number	*Inches*		*Number*	*Inches*		*Number*	*Inches*	
July 31, or earlier	32	55	6	2	68	20	5	55	4
Aug. 1 to 4	25	65	25	5	84	34	4	79	22
Aug. 5 to 8	16	76	45	4	91	68	1	82	40
Aug. 9 to 12	9	82	68	3	96	75			
Aug. 13 to 16	8	97	79	3	113	82	1	107	85
Aug. 18, or later	1	120	95						

[1] The 4 dent hybrids listed in table 2 have not been included in this table, only the open-pollinated corns being considered.

A second correlation, between resistance and maximum height of the corn, was found within each varietal group. The tall varieties ordinarily showed greater resistance than the short ones. The coefficient of correlation between resistance and height for the sweet corn varieties, estimated with no regard for the earliness or lateness of the corn varieties, was $r=0.78\pm 0.027$. However, since the later varieties are usually taller than the earlier ones, as further discussed in the following paragraph, it was deemed necessary to consider the association of resistance with height only in groups of varieties which had the same silking date. Thus there were 19 sweet corn varieties which had the same silking date, August 2, but which differed in the maximum height they reached, from 38 to 82 inches. An examination of these varieties, listed in table 4, shows that the taller ones as a rule are more resistant than the shorter ones. For instance, Whipple White, Extra Early Adams, and Golden Rod, show considerably greater resistance than Mammoth White Cory, Surprise, Extra Early Golden, and others. Early Sweet variety seems to be a conspicuous exception to the general rule as it showed a low degree of resistance in spite of its relatively great height. The same correlation, between resistance and height, was found within other sweet corn groups as well as within the dent and flint corns (figs. 1 and 2).

[4] In all statistical analyses, including estimates of odds for significance, use has been made of R. A. Fisher's Statistical Methods for Research Workers. Ed. 5, 319 pp., illus. Oliver and Boyd. Edinburgh and London. 1934.

A third correlation, that between lateness and height, already mentioned, has been commonly apparent among all varieties of corn.

FIGURE 1.—Differences in resistance to bacterial wilt between early and late corn varieties: *A*, Early, short, susceptible flint variety, destroyed by bacterial wilt; *B*, late, tall, resistant, dent variety.

Kuleshov (*3*) pointed out this correlation through a study of a world-wide collection of corn varieties of all types. He observed further

that the long-season varieties had a greater number of leaves than the short-season ones, although there were some exceptions to this rule.

FIGURE 2.—Kutias, a late, tall, flint variety, highly resistant to bacterial wilt: *A*, Control row; *B*, inoculated row.

The coefficient of correlation between height and lateness based on the measurements on the 92 sweet corn varieties employed in the present studies was $r=0.73\pm0.032$.

TABLE 4.—*The relation between height and resistance to bacterial wilt in sweet corn varieties having the same silking date*

Variety	Maximum height	Index of resistance	Variety	Maximum height	Index of resistance
	Inches			*Inches*	
Mammoth White Cory	38	0	Golden Giant, De Lue's	69	66
Surprise	46	0	First of All, Maule's	70	45
Extra Early Golden	47	0	Early Sweet	71	14
Portland Market	52	0	New Jersey Early White	73	44
Early Surprise	52	5	Howling Mob	76	51
Columbia	55	0	Golden Giant	77	46
Carmel Golden	58	8	Golden Rod	80	40
Ford Early	60	15	Extra Early Adams	80	53
Golden Bantam	62	15	Whipple White	82	70
Mayflower	69	37			

The coefficients of the three simple correlations just considered for the sweet corn varieties appear higher than those for inbred strains of the Golden Bantam type as reported by Ivanoff and Riker (*2*). The reason for these differences most probably is the fact that the inbred strains have been tested and selected for resistance during three seasons, and during these processes a great number of the early susceptible and the late resistant strains have been eliminated, while the number of relatively early resistant strains has been enlarged.

A comparison in the resistance of the sweet, dent, and flint corn varieties was made in the light of recent studies. Since it was found that resistance is positively correlated with the lateness and height of most varieties, an attempt was made to determine what influences these two plant characters might have upon the greater resistance of the field corn varieties grown in the Middle West. It should be noted in this connection that lateness and height are not necessarily considered to be the cause of resistance, but only correlated with it. The three varietal groups were arbitrarily divided into six categories on the basis of the progressive lateness of the corn. By this arrangement the resistance of groups of sweet corn varieties of a certain lateness could be compared with the resistance of the dent and flint corn varieties of approximately the same lateness, as shown in table 3. This table reveals that the indexes of resistance of the dent corn varieties for each category are in most cases somewhat higher than those of the sweet and flint corn varieties. The same table also shows that the dent corn varieties of the various categories are from 5 to 19 inches higher than the sweet and flint corn varieties. These differences in height, owing to grouping of a relatively small number of varieties, might easily account for the slightly higher resistance of the dent corns just mentioned. However, when some individual sweet, dent, and flint varieties having exactly or almost exactly the same height and exactly the same silking date, are compared for resistance (tables 1 and 2) the differences in the indexes of resistance among the three varieties become insignificant.

Further statistical analysis of the resistance of the sweet, dent, and flint corn was made by calculating the partial correlation coefficients, in addition to the simple ones, and by testing the various coefficients and the differences between them for significance. The results of these calculations are included in table 5.

TABLE 5.—*Simple and partial correlation coefficients among resistance, silking date, and height of sweet, dent, and flint corn*

Kind of correlation	Plant characters correlated [1]	Sweet corn		Dent corn		Flint corn	
		Number of variables	r (coefficient of correlation)	Number of variables	r (coefficient of correlation)	Number of variables	r (coefficient of correlation)
Simple	RM	92	0.860**	21	0.847**	11	0.980**
	RH	92	.784**	21	.816**	11	.902**
	MH	92	.733**	21	.773**	11	.902**
Partial [2]	RM:H	92	.678**	21	.591**	11	.902**
	RH:M	92	.445**	21	.478*	11	.214
	MH:R	92	.316**	21	.267	11	.214

[1] R=Index of resistance.
M=Maturity (silking date).
H=Height.
*P value (level of significance) exceeds the 5-percent point.
**P value exceeds the 1-percent point.
[2] Correlation between 2 characters when holding the effect of the remaining character constant.

The differences among the simple correlation coefficients of the sweet, dent, and flint corn for the same pair of characters was not found to be significant. Likewise no significant differences were found among the partial correlation coefficients of the three types of corn for the same pair of characters. It appears, therefore, that resistance is correlated with silking date and height to a high, and approximately the same degree, within each type of corn. The relatively higher resistance of the most dent corn varieties grown in the Middle West is not because of any type of resistance inherent in these varieties and lacking in the sweet and flint types, but because of the relatively greater height and lateness characteristic of the dent corn varieties grown in that region.

SUMMARY

Ninety-two sweet, 17 dent, and 11 flint corn varieties were tested for resistance to bacterial wilt by artificial inoculation.

Great differences in resistance were found within each of the three varietal groups of corn.

A high correlation was found between resistance and height, resistance and lateness, and height and lateness in each varietal group.

The dent corn varieties of a certain lateness and height were found to be no more resistant than sweet and flint corn varieties of the same lateness and height.

It appears that the resistance of open-pollinated field corn is similar in type and degree to that of open-pollinated sweet and flint corn.

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RESISTANCE TO BACTERIAL WILT OF INBRED STRAINS AND CROSSES OF SWEET CORN[1]

By S. S. IVANOFF, *research associate in plant pathology*, and A. J. RIKER, *professor of plant pathology, Wisconsin Agricultural Experiment Station*[2]

INTRODUCTION

The bacterial wilt disease of maize (*Zea mays* L.) caused by *Phytomonas stewarti* (Smith) Bergey et al. in recent years has been one of the most serious diseases of sweet corn in the United States.[3] Attempts to control the disease by developing resistant varieties seem to offer greater promise than other measures, and perhaps the only promise. The present report summarizes the results of 3 years' studies on the resistance to bacterial wilt of more than 2,000 inbred lines and crosses of the Golden Bantam type of sweet corn.

Many reports on bacterial wilt have appeared since Stewart *(17)*[4] discovered the disease in 1895. The first observations on resistance of open-pollinated varieties of corn to bacterial wilt were made by E. F. Smith (*15*) in the summer of 1903, when the disease was very prevalent near Washington, D. C. Smith found that among the approximately 30 sweet-corn varieties tested, infection varied from 0 to 66 percent and that infection was greatest among the early varieties. The late varieties suffered little or no damage. Smith's findings were confirmed by the more extensive trials of Rand and Cash (*12, 13*). Thomas (*18*), who tested the resistance of 39 open-pollinated varieties of sweet corn under conditions favorable for natural infection and development of the disease, observed a tendency for the resistant quality to be reduced when selections were made for earlier maturing strains. For instance, while the Fordhook variety showed marked resistance, Early Fordhook under the same conditions showed more than 10 percent infection. Early Adams was somewhat resistant while Extra Early Adams was susceptible. Similar results, with some exceptions noted, were obtained in later studies by Mahoney, Muncie, and Marston (*11*), Clinton and Singleton (*1*), G. M. Smith,[5] and others.

Many investigators have worked on the resistance of inbred and hybrid corn to bacterial wilt. Reddy and Holbert (*14*) tested by artificial inoculation the resistance of 15 inbreds of yellow dent corn and 4 of their recombinations, all maturing in approximately the same number of days. The differences in resistance were estimated by the mean percentage reductions in yield of ear corn. The first generation crosses were found to be more resistant than their component inbred strains, and all the progenies of some of the inbred

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[3] UNITED STATES DEPARTMENT OF AGRICULTURE, BUREAU OF PLANT INDUSTRY. [BACTERIAL WILT OF SWEET CORN.] U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Reptr. 16-19. 1932-35. [Indices should be consulted for specific pages.]

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lines tested were uniformly high in resistance. On the basis of these results Reddy and Holbert suggested the possibility of developing resistance to bacterial wilt in some of the popular wilt-susceptible varieties of sweet corn. Ivanoff and Riker (*7*, *8*) and Ivanoff, Riker, and Dickson (*21*, *22*) in preliminary notes reported a correlation between resistance and vigor on the one hand and resistance and lateness on the other, among inbred strains of Golden Bantam sweet corn. They stated that, after taking into consideration the factors for vigor and lateness of the strains, it commonly appeared that crosses between susceptible inbreds gave susceptible hybrids; that crosses between susceptible and resistant inbreds gave resistant hybrids; and that crosses between resistant inbreds gave resistant hybrids. They also reported that hybrid vigor is responsible for some resistance. Wellhausen (*19*, *20*) made genetic studies on resistance in 56 inbred lines of field, flint, and sweet corn, and 14 crosses made from these lines. He found that the inbred lines varied in resistance from highly susceptible to highly resistant. The majority of the field-corn inbreds were resistant; the majority of the inbreds of the Evergreen group of strains were intermediate in resistance; and the majority of the early sweet-corn inbreds were susceptible. The crosses tested for resistance were made mostly between highly resistant field-corn inbreds and very susceptible sweet- and flint-corn inbreds. Wellhausen reported that he found resistance to be dominant in all F_1 material tested and that in a few cases the F_1 hybrids were more resistant than either of the parents. He also reported the results of F_2 and backcross tests of two hybrids (highly resistant field-corn parent $\times$ very susceptible flint-corn parent, and highly resistant field-corn parent $\times$ very susceptible sweet-corn parent) which showed a definite segregation of factors for resistance, with a strong indication that two major dominant complementary genes, with perhaps a third modifying gene, were involved in resistance. However, in making and testing the various crosses for resistance, Wellhausen does not seem to have taken into consideration the usual association of the characters for lateness and height of the host with its resistance, and particularly the lateness and height of the crosses as compared with those of the composing inbreds. Wellhausen also found differences in the reaction of the fibrovascular bundles to bacterial invasion among the different susceptible lines of corn.

Mahoney and Muncie (*10*), in a report of trials on resistance in which they employed inbred strains and hybrids, raise the question whether resistance to bacterial wilt is heritable. Their conclusions seem to indicate that wilt resistance in corn is governed mainly by the vigor and rate of growth of the tested plants, the more vigorous and the more rapidly growing plants being able to outgrow the disease more easily than the less vigorous ones. They also point out the important fact that initial infection is not a measure of resistance, for ordinarily resistant lines in the course of time outgrow the disease.

The purpose of the present investigation is to clarify the principles involved in the resistance of sweet corn to bacterial wilt and thereby to facilitate the development of disease-resistant hybrids. The results herein reported are concerned mainly with the following three phases of the problem: (1) Degree of resistance; (2) correlation of resistance with certain plant characters; and (3) modes of inheritance of resistance. Preliminary accounts of a part of these studies have already been given (*7*, *8*, *21*, *22*).

MATERIALS AND METHODS

Some of the preliminary inoculation tests were started in 1931 on the trial plots of the Wisconsin Agricultural Experiment Station, at Madison, Wis. (*3*). The main resistance trials were started in 1933 and continued through 1934 and 1935. These were conducted near Rochelle and De Kalb, Ill.

The corn used in the experiments was as follows: In 1933, about 430 inbred strains, approximately 200 hybrids, and 30 open-pollinated varieties of sweet corn; in 1934 about 900 inbreds and approximately 350 hybrids and top crosses; and in 1935 about 600 inbreds and 350 hybrids and top crosses and a large number of commercial crosses and open-pollinated varieties. Nearly all of the inbreds and crosses were derived from open-pollinated Golden Bantam corn and about one-third of them were of the true Golden Bantam type, the ears having eight rows of kernels. Most of the Golden Bantam lines used had been inbred for 6 or more years.

Of the corn tested from season to season as a whole the following may be said: The inbreds tested in 1935 were practically the same as were tested in 1933 and 1934, with the exception of those which were eliminated in the course of the trials because of extreme susceptibility and those which were further selected for their resistant qualities. The hybrids, on the other hand, represented to a large degree new material each year. Genetically, so far as resistance is concerned, the hybrids as a group differed considerably from season to season. Thus, the hybrids tested in 1933 and 1934, particularly those tested in 1933, were produced at a time when the resistance of their respective parent inbreds was not well known. These parents consequently in the majority of cases possessed a low degree of resistance, as was shown by the data obtained in 1933 and 1934. On the other hand, the hybrids tested in 1935 were made from inbreds most of which were already known to possess a high degree of resistance. Since the resistance of the hybrids seems to be influenced by the resistance of the parent inbreds, as already reported in preliminary notes by Ivanoff, Riker, and Dickson (*21*, *22*), the hybrids tested in 1935 were on the whole considerably more resistant than the hybrids tested during the previous two seasons. These differences in the hybrid material tested each year must be borne in mind as they have a bearing on the interpretation of some of the results in this report.

In 1933 each line of corn was usually represented by one row of approximately 45 plants, and in 1934 and 1935, by two rows each of about the same number of plants. Some of the lines were replicated from two to five times, others were represented by a larger number of individuals than stated above, while still others, because of unfavorable conditions for germination (particularly during the cold, wet early spring of 1935), had fewer than the usual number.

In addition to the above-mentioned replications, four varieties of corn were replicated from 10 to 30 times throughout the experimental field. These were Golden Gem, Golden Bantam, Purdue Bantam, and Golden Cross Bantam (*16*). The reaction of the replicates to the disease are reported under Preliminary Trials.

The resistance of the corn strains was tested by artificial puncture inoculation and by natural infection, when that occurred. These two methods of testing for resistance seemed to strengthen each

other, and so far no incompatibility between them has been noted, although such incompatibility may sometime occur, as will later be shown. Under the conditions of these trials artificial inoculation was considered to provide a more dependable means for measuring resistance, and during the last two trial seasons it was the only method available.

The plants were inoculated with an instrument described earlier by Ivanoff (*4*). By the use of this instrument eight men were able to inoculate approximately 100,000 plants in 2 days. The usual method of puncture by means of an ordinary needle was entirely inadequate because progress was too slow and the inoculations thus made were not uniform. The use of a common hypodermic syringe for inoculation of corn plants was found unsatisfactory because the needle plugged frequently, the plunger was slow and inconvenient to operate, and ejection of small uniform amounts of inoculum was difficult. Inoculating a great number of plants in a relatively short time and in a uniform manner is particularly important in resistance trials where small variations in resistance are to be secured. It must be borne in mind that the age of the plant influences the degree of infection considerably and a delay in inoculation of a week or 10 days in many cases may lead to confusing results.

The plants were inoculated by making two punctures at the base of each. The thrusts, which passed entirely through the culm, were made crisscross one above the other about 1 inch apart. In this manner of inoculation the introduction of the bacteria into the plant was well insured.

Some of the plants of each corn strain were inoculated and some were left uninoculated as controls, or for tests through natural infection. In 1933 about two-thirds of each row, or about 30 plants, were inoculated, and about 15 plants were left untreated. In addition, most of the material was replicated on another plot where the strains were subjected to natural infection only. In 1934 and 1935 the plants in one row (about 45) were inoculated, while those in the other row served as checks. In a few cases puncture controls were made with sterilized water instead of bacterial suspension, but the plants so treated showed no difference from unpunctured plants.

In all trials inoculations were made at two different times. The first were made during the most susceptible stage for most of the corn strains, about 5 to 6 weeks after planting, the exact time depending upon the growing conditions and upon the condition of the host. The second inoculations followed the first in about 2 weeks.

Five cultures, representing various types of wilt-producing bacterial organisms, were used to inoculate the plants (*3*). These cultures were selected to insure infection in susceptible plants with the various diseases known as Stewart's wilt, bacterial wilt, and bacterial stalk rot, as defined by Ivanoff (*5*). At least three of the five cultures were progenies of single bacterial cells; the others were purified by plating. Three or four of the cultures used were derived from diseased material obtained from the State of Illinois, while one or two of the others, although they occur naturally in Illinois, were isolated from diseased corn plants grown in eastern States. One of the Illinois cultures was usually freshly isolated from naturally diseased material shortly before the inoculations were made. The pathogenicity of the

cultures was tested on corn plants in the greenhouse some days before they were used in the field. The various cultures were grown separately on nutrient dextrose agar plants in 12-ounce bottles, and a mixed standardized suspension made from 3- to 5-day-old cultures was prepared at about ½-hour intervals during the time of inoculation in order to keep the suspension fresh. The turbidity of the suspension was approximately equal to that obtained by mixing 97 cc of 1-percent sulphuric acid solution with 3 cc of 1-percent barium sulphate solution (suspension no. 3 of McFarland nephelometer (*9*)). Although the degree of pathogenicity of some of these cultures varied on the same host, so far the inoculation tests have not shown that these cultures represent different specialized races such as are known to occur with *Puccinia graminis* Pers. and some other pathogens. Likewise no appreciable antagonism has been noted among the various cultures in the combinations employed.

The following records of the plants were kept: (1) Degree of resistance, (2) length of the period to maturity, and (3) height at three different intervals, including that at the time of maturity.

The degree of resistance of each inoculated plant at a certain time was estimated on the basis of disease injury to the plants. Each plant was given one of the following five indices of resistance: 0, 25, 50, 75, and 100. These corresponded to five more or less distinct degrees of disease injury, estimated (1) by the condition of all the leaves, (2) by the degree of stunting and corresponding ear development, and (3) in some cases, by the condition of the inside stalk tissues. A plant which at the time of record taking was found to be dead, with all of its parts dry and light brown in color on account of the disease, was very stunted, and had a very small ear or no ear at all, received an index of resistance of 0, while a plant which appeared normal, like the uninfected control plants of the same strain (even though the bacteria were present within its tissues), received an index of resistance of 100. Between these two extreme degrees there were plants which exhibited three other marked degrees of wilting. These were given an index of resistance of 25, 50, and 75. Thus a plant which was considerably stunted, with about one-half of its leaves dry and light brown, with its stalk still green, and with a small ear received an index of resistance of 25. Another plant, less stunted, with most leaves green but considerably striped, and with an ear about one-half the size of normal, received an index of 50. A plant only slightly stunted, with all leaves green, mostly free from stripes, with an ear slightly below normal, received an index of 75. The index of resistance for an entire strain was stated as the mean of the indices of all the plants of that strain. These indices corresponded roughly to the percentage yield at the time of harvesting the corn. The final records on resistance were taken at the time that most of the corn ears reached canning stage. This last point is discussed later.

All records were taken by number without reference to the identity of a strain or its past performance.

The length of the period to maturity (the lateness or the earliness) of the inbred lines was measured by the date of silking, and in the case of the hybrids, by both the date of silking and the date of harvesting for canning. The silking date of a line was the date on which 75 percent of the corn plants of that particular line came into silk. This method of determining the earliness or lateness of a corn strain has

been used by Huelsen and Michaels[6] and found to be very satisfactory. Its dependability was confirmed in these studies by a comparison between the silking dates and the harvesting dates for the same strains of corn.

The height of the corn of the different strains was measured at three intervals, that is, at the time of the two inoculations and after the plants had reached their maximum height. The height and maturity measurements were made on the uninoculated control plants.

The degree of reaction to the inoculations of the strains as a whole differed during the 3-year trial. In 1934 and 1935, because of the earlier inoculations, and because of favorable environmental conditions following the inoculations, the plants were affected to a higher degree than in 1933. Correspondingly, the average index of resistance of the strains in 1934 and 1935 was considerably lower than in 1933 for the same strains. However, on the whole the relative resistance of the various strains during the three seasons' trials was maintained. Thus as a rule strains which showed a relatively high index of resistance in one season showed a relatively high index of resistance in the other two seasons. Likewise, strains which were very susceptible in 1933 were among the first to go down with the disease in 1934 and 1935.

Unless otherwise stated the indices of resistance of the various inbreds and hybrids given in this paper are those for 1934.

The term "resistance" as used in this paper implies the ability of the host plant to continue a more or less normal development in the presence of the pathogenic bacteria within its tissue. Medium-resistant and high-resistant lines mentioned in this paper indicate relative degrees of host resistance as defined above. The term "resistance" excludes cases of immunity. No immune corn plants have yet been found; i. e., no plants after being either inoculated at an early stage or subjected to conditions favorable for natural infection at an early stage, have failed to develop leaf stripes on the first few leaves.[7]

PRELIMINARY TRIALS

The results of a number of earlier inoculation trials, together with some observations made in the course of these studies, because of their preliminary character, are reported at the outset. They contribute toward a better understanding of the methods employed and of the interpretation of data given in Experimental Results. These trials and observations were on: (1) Comparative efficiency of various methods of inoculation, (2) period of greatest host susceptibility, (3) age of host plant in relation to type of symptom expression, (4) comparative rate of wilting of hybrids and their respective inbred parents, (5) determination of time for final record taking, (6) uniformity of inoculation, and (7) comparison between artificial puncture inoculation and natural infection. The detailed experimental data are omitted because of their volume.

[6] HUELSEN, W. A., and MICHAELIS, W. H. THE EFFECT OF MATURITY ON THE YIELD COMPLEX OF SWEET CORN. (Unpublished manuscript.)

[7] High degrees of resistance to the disease have been shown by nearly all the sorghum, common millet, German millet, Sudan grass, and yellow foxtail plants tested thus far (*5*). The plants usually developed leaf stripes and occasionally some symptoms in the culm when artificially inoculated at an early stage, but they soon recovered with little or no apparent effect on yield or vigor. On the other hand, some varieties of wheat, barley, oats, sugarcane, and other grasses appeared immune to the disease, as they developed no leaf or other symptoms following inoculation.

A number of different methods of inoculation were tried on open-pollinated Golden Bantam corn in the greenhouse and the field. These methods consisted of (1) applying drops of inoculum on the tips of the leaves and in the spiral whorl of young seedlings, (2) atomizing punctured and unpunctured leaves, (3) smearing the inoculum on the seeds, (4) puncture-inoculating the kernels, and (5) puncture-inoculating the young plants at the base. The various trials were repeated three or more times and involved from 300 to several thousand plants. Of all the methods tested, puncture-inoculating the young plants at the base was the most effective. By this method many thousands of young plants were inoculated at a susceptible stage and in no case did the characteristic leaf stripe symptoms (*3*) fail to appear. These stripe symptoms, however, may fail to become evident, or may easily be overlooked in cases when (1) the plants have become infected at a late stage, (2) the plants have become infected at a very early stage (about a week or so after planting) and rot-producing bacteria, other than, or in addition to *Phytomonas stewarti*, have established themselves in the plant tissue, (3) the wilt bacteria after entering a seedling plant have failed to establish themselves systemically before the emergence of the tassel (delayed systemic infection), and (4) in exceptionally susceptible strains, the discoloration of the entire leaf tissue has taken place at an extremely rapid rate. These cases, some of which are relatively rare in nature, have been avoided in the resistance studies by adapting the methods of inoculation already described.

The period during which the corn plant is most susceptible to infection induced by puncture inoculation at the base of the plant was determined. Through a series of trials during five seasons, in which several corn varieties and inbred strains were tested, it was found that the plants were most susceptible when 3 to 6 weeks old. Later inoculations with some varieties resulted in a distinctly lower degree of infection. On the other hand, if the inoculations were made when the plants were very young, 1 to 2 weeks old, there was occasionally a low degree of infection, delayed systemic infection, or none. This probably was because of the small number of leaves punctured, which, at that stage of host development, withered and died before enough, if any, of the bacteria were able to reach the stem bud tissue. It was not so much the age of the plant as its degree of development that was important for susceptibility. Cold weather may retard the development of the growing plant considerably, in which case plants 5 weeks old may have reached only their five-leaf stage. In such cases later inoculations gave better results. Inbreds and hybrids of the Golden Bantam type were found to be very susceptible in their seventh- to tenth-leaf stage, when 16 to 20 inches high. At this stage the stem tissue is usually just emerging above the soil line. In the resistance trials a great many strains of corn were inoculated some of which developed more slowly than others. The corn plants were therefore inoculated twice during the growing period so as to make sure of striking the period of greatest susceptibility of each line at least once.

The age of the plants was found to determine not only the degree of infection, but also the type of symptoms that developed. Corn plants inoculated before the emergence of the tassel developed the characteristic leaf-stripe symptoms of the disease. These symptoms appeared

whether the puncture passed through the leaf sheaths and the unfolding leaves alone, or through the tissue of the growing stem as well. In older plants, after the tassel and all the leaves had emerged, the leaf stripes usually did not appear following inoculation at the stem. The leaves of the susceptible corn strains inoculated at this late stage withered gradually and the color changed from green to light brown, whereas the leaves of the highly resistant strains remained more or less normal in color. Naturally infected plants of relatively susceptible open-pollinated varieties in some seasons exhibited a gradual, diffuse type of wilting without showing the characteristic leaf stripes. Such plants are commonly considered either to have become infected at a late stage, or, more rarely, to represent cases of delayed systemic infection from very early infection.

The rate of wilting, independent of the degree of resistance, of the hybrids in relation to that of their respective inbred parents was investigated because of its importance in determining the time for taking the final records on resistance and in interpreting the results. Consequently, tests were undertaken with about 100 hybrids to determine the respective rate of wilting of hybrids and parents under conditions of severe infection, the latter being measured by the performance of standard corn lines.[8] The results showed, that in most cases there was no appreciable difference in the rate of wilting of parents and hybrids throughout the season. Such differences may be brought about, however, in the case of susceptible lines and hybrids if the inoculations have not been severe enough.

The time for taking the final records is important in the evaluation of the strains for resistance. It was thought desirable to delay the record taking as much as possible in order to allow the bacteria to have full play in association with the host. Since the first symptoms following inoculation appeared on the leaves of both susceptible and resistant strains, too early record taking tended to equalize the differences among the strains. Later in the season these differences usually became more apparent, the susceptible strains gradually going down with the disease and the resistant strains gradually coming out of it. On the other hand, too great a delay in taking the notes on resistance may lead to difficulties and even confusion because of the natural discoloration and withering of the leaves at later stages of plant maturity. It was found that the best time for taking the final records on resistance was when the corn reached canning stage, which for the Golden Bantam variety, was about 70 to 75 days after planting, and about 40 to 45 days after the first inoculation. By that time the disease on the various corn strains had reached a more or less stationary stage of development.

The uniformity of inoculation was demonstrated by the more or less uniform degree of infection produced in highly inbred lines, in related lines, and in replications of certain lines of corn. In the very susceptible lines practically all of the individual plants died at the same rate throughout the season, and in the highly resistant lines, the slight wilting was approximately the same in each plant. Among the plants of certain intermediate lines some variations in resistance were observed. In the summer of 1934, however, there were exceptions to

[8] By severe infection is meant infection which causes more than a 75-percent loss in yield of open-pollinated Golden Bantam corn at time of harvesting for canning. Other varieties and crosses, such as Golden Gem, Purdue Bantam, and Golden Cross Bantam have also been used to measure severity of infection.

these rules, evidently because of the presence of other diseases toward the end of the season, such as smut and fungus stalk rots. There were some variations in the reaction to the inoculations among the several replications of certain lines. The index of resistance of about 15 replications of a line varied from 0 to 10 points from the mean, most of the values being distributed closely around the mean. The more conspicuous variations, however, were probably due more to the effect which soil and land incline may have upon the host than to the inoculation technique, for when two or more rows of the same line of corn were planted near each other, the variations among them were hardly noticeable.

The correlation between infection produced by artificial inoculation of certain lines of corn and that occurring naturally in the field in the same lines of corn was of particular importance in these studies. Since bacterial wilt of corn is epidemic in character, occurring in some seasons to a considerable degree and being almost entirely absent in other seasons in the same locality, artificial inoculation in the continued testing for resistance of corn lines was necessary. Such inoculation would be of doubtful value in measuring resistance, however, if the infection thus induced in relatively resistant and susceptible lines of corn did not correlate with the infection produced in the same lines of corn through natural agencies. Such correlation was demonstrated to exist in 1933, when natural infection was widespread early in the season in fields of Golden Bantam corn as well as in the experimental plot. Thus inbred strains in which the inoculated plants had an index of resistance of 0 or near 0 showed the highest degree of injury from natural infection. Likewise, many strains which had a high index of resistance remained relatively unaffected by the disease through natural infection. Among the commercial varieties of corn the same relation existed. Thus, Country Gentleman, Golden Cross Bantam, Golden Bantam, and Golden Gem showed in this order decreasing degrees of resistance both from artificial inoculation and from natural infection. The same varieties have been known by corn growers to hold the same relative position in regard to resistance during previous years when the disease has been widely prevalent. Additional evidence on the correlation of results obtained by artificial inoculation and natural infection was gathered in the summer of 1935, when approximately 25 open-pollinated varieties, previously tested for resistance through natural infection in three different seasons by Rand and Cash (*12*, *13*), were again tested by artificial inoculation (*6*). When these varieties were arranged in the order of their resistance, as determined by artificial puncture inoculation, the order was found to approximate that for the same varieties made by Rand and Cash on the basis of natural infection.

As a method of testing resistance natural infection has some serious disadvantages, such as (1) it takes into account only the strains of the causal bacteria that happen to be present locally; (2) it may occur in widely varying degrees from season to season, and at different places in the same field during the same season (*13*); (3) the conditions for its severest development may occasionally occur after the period of greatest susceptibility for some strains, in which case early susceptible strains may escape damage, while later, and relatively more resistant, strains may show considerable injury (*10*); and (4) individual plants even at their most susceptible stage may escape the disease. Arti-

ficial inoculation was found to have the following advantages over natural infection: (1) Infection was induced at the most susceptible stage of the host; (2) all plants became infected at the same time; (3) infection was uniform; (4) escapes were avoided; (5) the type and amount of the inoculum was standardized; and (6) the inoculating suspension contained representatives of all the known types of the causal bacteria. By artificial inoculation severe infection was induced even when the conditions for natural incidence of disease were very unfavorable, as was the case in 1934 and 1935.

EXPERIMENTAL RESULTS

The experimental results reported here are of representative trials and give the general summary of three seasons' studies, mainly on the resistance of the inbred lines and experimental hybrids. For the sake of brevity, detailed accounts of many repeated experiments have been omitted. For the same reason it has been thought advisable to give as representative the tabulated data from 1 year's trials (1934), supplementing these data by those of the other two seasons' trials only when necessary for further clarity.

FIGURE 1.—A number of inbred strains of sweet corn inoculated with wilt-producing bacteria. Some of these strains tolerated the activities of the bacteria better than others.

Because of the similarity in the results between the F_1 hybrids and top crosses in regard to the general principles governing resistance, no tabulated data on the top crosses have been included.

RESISTANCE OF INBRED LINES

Significant differences in resistance among the inbred lines of sweet corn were found (fig. 1). Some of the strains wilted and died shortly after inoculation without being able to produce ears, while others reached maturity without any appreciable loss in either yield or vigor. The majority of the inbred strains, however, showed degrees of resistance intermediate between these extreme limits.

The taller strains as a rule showed greater resistance than the shorter strains, as may be seen from table 1.[9] In this table each of three groups of inbreds, comprising relatively early- medium- and late-maturing strains (as determined by the silking date), has been divided into four classes according to the maximum height they reached and the average index of resistance. It is evident that as the height of the inbreds increases from class to class, so does the index of resistance for each class. Table 1 shows that there is a definite correlation between the height of the strains and their resistance, and, correspondingly, that a resistant line is more likely to be found among the tall-growing, vigorous inbreds than among the short, weak ones (fig. 2). However, there were some tall-growing and vigorous-appearing strains (also included in the table) which showed little resistance to the disease (fig. 3). It appears, then, that one cannot be sure of the resistance of any particular tall and vigorous inbred, unless it has been thoroughly tested.

TABLE 1.—*Relationship between height and date of silking, respectively, with index of resistance of sweet corn inbreds of the Golden Bantam type, in 1934* [1]

Silking date [3]	Index of resistance for inbreds of maximum height indicated [2]								Total or average	
	35 inches or below		36 to 47 inches		48 to 59 inches		60 inches or above			
	Inbreds	Index of resistance	Inbreds	Index of resistance	Inbreds	Index of resistance	Inbreds	Index of resistance	Inbreds	Index of resistance
	Number		*Number*		*Number*		*Number*		*Number*	
Aug. 9 or earlier	4	10	50	29	49	36	4	71	107	31
Aug. 13	6	31	107	34	71	50	18	61	202	42
Aug. 21 or later	3	22	32	37	26	55	7	72	68	47
Total or average	13	22	189	33	146	46	29	65	------	------

[1] Similar results were secured in 1933 and 1935.
[2] The average height of the 4 groups of inbreds at the time of the first inoculation (5 weeks after planting) was 15, 16, 17, and 18 inches, respectively. These slight differences in height are not considered to have significant influence on the final results.
[3] All corn planted June 11.

The later inbreds as a rule showed greater resistance than the earlier ones. This relation between lateness and resistance has been observed by other workers, already mentioned, in a number of open pollinated varieties of corn. These workers, however, have not taken into consideration the height of the plants, and a correlation between lateness and resistance cannot be very exact unless it is made among strains of approximately the same height and type, as will be explained later. In table 1, such a correlation is shown within the groups of inbreds of approximately the same height that are large enough to have statistical significance.

There were several relatively early strains among all those tested, the resistance of which was not correlated with height or lateness or, so far as could be determined, with any other plant character. These strains were approximately as early as open-pollinated Golden Ban-

[9] Height at maturity has been generally considered to be the best single measure of the vigor of a strain of corn, but since not every tall strain could be considered as vigorous, the writers prefer to use height rather than vigor when correlating this plant character with resistance.

tam, were not very tall, but showed a high degree of resistance. The resistance of such strains, for lack of a better term, has been called "true resistance." This resistance may be considered as a distinct type and may exist in different degrees within most of the strains. The degree of this type of resistance, within a particular late corn

FIGURE 2.—Two inbred lines of sweet corn inoculated with wilt-producing bacteria. The inbred line on the right was tall and showed a considerably higher degree of resistance than the short line on the left. A high correlation was found between resistance and height of the inbred lines.

strain, however, would be difficult to determine on account of the masking effect of the characters of height and lateness and the resistance associated with them.

In addition to the correlation between resistance and height and between resistance and lateness, a third correlation was found among

certain groups of inbred strains between height and lateness. This correlation is an important factor in resistance trials because of its heretofore confusing influence in the matter of determining the exist-

FIGURE 3.—Two tall and vigorous inbred lines of sweet corn of approximately the same height and maturity inoculated with wilt-producing bacteria. The one on the left was very susceptible, while the one on the right was very resistant. Tall, vigorous inbreds susceptible to the disease are rare.

ence and extent of the two distinct correlations in resistance just mentioned. However, its interference in the interpretation of the results of these studies has been avoided by segregating the strains

in groups according to lateness and height, as shown in table 1, and by the use of partial correlations.

Simple, partial, and multiple correlation coefficients were calculated for the characters of resistance, lateness, and height of approximately 860 inbred strains tested in 1934.[10] The simple correlations between resistance and height on the one hand, and resistance and lateness on the other were 0.496 and 0.519, respectively. The partial correlation coefficients for the same pairs of variables when holding the effect of the remaining variable constant, were respectively 0.643 and 0.674. In all four cases the value of P (level of significance) exceeds the 1 percent point. The multiple correlation coefficient for these inbred lines was $R=0.768$, indicating that the resistance of the average inbred is highly correlated with its height-lateness character complex, and that there is an additional degree of resistance that is not correlated either with height or lateness.

RESISTANCE OF F_1 HYBRIDS

The hybrids, like the inbreds, varied greatly in resistance to bacterial wilt. Some were as susceptible as the open-pollinated Golden Bantam variety and succumbed to the disease early in the season, while others reached the canning stage without any appreciable loss in yield or vigor.

An attempt was made to determine the principles governing hybrid resistance by analyzing the data gathered in the three seasons' trials. Attention was directed particularly to the possible correlation of resistance with height and lateness, to inheritance of resistance, and to the dominance relationships of resistance. The plan of presenting the data on hybrid resistance is briefly as follows: (1) Influence of height and lateness of hybrids on hybrid resistance; (2) influence of inbred parents' resistance upon hybrid resistance; (3) the dominance relationships of resistance; and (4) certain important exceptions to the general rules regarding hybrid resistance.

Because of the great number of hybrids studied (approximately 1,000), it is not feasible to consider each individually. Instead, detailed consideration is given only to a relatively small group of representative hybrids by means of which the major points are illustrated. This study is supplemented by a group study of the hybrids as a whole. The 36 hybrids comprising this representative group each had one inbred parent, M, in common. Thus they were genetically more closely related than the hybrids as a whole; they showed considerable differences in height, lateness, and index of resistance.

Influence of Height and Lateness of Hybrids on Hybrid Resistance

The relation of hybrid resistance to height and lateness is considered in the representative group of hybrids listed in table 2. These hybrids are divided first into tall and short, and later into early and late, the dividing line being the average value for height and the date of harvesting for canning, respectively. It appears from the indices of resistance that on an average the taller hybrids are more resistant than the shorter, and the late more resistant than the early. Thus the tall hybrids have an average index of resistance of 43 and the short

[10] In all statistical analyses use has been made of Fisher's Statistical Methods (2).

hybrids one of 37. Likewise the early hybrids have an index of resistance of 25 and the late hybrids one of 50. The differences in the indices of resistance between the groups would undoubtedly have been greater if only the extreme cases had been considered. While it appears that height and lateness are generally associated with greater resistance, as was noted among the inbreds, there are still significant differences in the indices of resistance, up to 56 units, among the individual hybrids of each group. However, when the same 36 hybrids were again classified into two groups, this time on the basis of the two combined plant characters, namely, into tall, late hybrids and short, early hybrids, the differences in the indices of resistance among the individual hybrids within each group became somewhat narrower. (The table showing this grouping, for the sake of brevity has been omitted.) Yet significant differences in resistance among the individual hybrids within each group still existed which could not be accounted for by the combined effect of the height and lateness characters alone. It appears, therefore, that still another factor or factors associated with resistance must be sought.

Influence of Inbred Parents' Resistance Upon Hybrid Resistance

Next the possible influence of the inbred parents upon the hybrids is considered. In table 3 the same 36 hybrids are reclassified into three groups on the basis of the degree of resistance of the parent inbred which, together with parent M, went into the making of each of these hybrids. The index of resistance of the common parent M was 36, while that of the other parents varied in the three groups respectively from 0 to 25, 26 to 50, and more than 50. The average index of resistance for the hybrids of each group was 35, 34, and 61 respectively. The data indicate that, on the average, the resistance of the hybrids is dependent on the resistance of the inbred parents in general, and upon the more resistant of the two parents in particular. (Additional data concerning this point are presented later.) However, as in table 2 the individual hybrids in each group differ considerably among themselves in regard to resistance. But it has already been brought out that the resistance of this particular group of hybrids is correlated in addition with the height and lateness of the hybrids. It seems desirable, therefore, to examine the data with these three characters separated.

The evidence presented so far suggests that as a rule the resistance of a hybrid is influenced by at least three major factors, viz, height and lateness of the hybrid and resistance of the parents from which the hybrid was made. Continuing this line of analysis, each group of hybrids in table 3, in which the hybrids have already been classified on the basis of parental resistance, was further arranged on the basis of height and lateness into four subgroups as follows: Tall-late, short-late, tall-early, and short-early. The results of this arrangement are shown in table 4. From table 4 it is seen that, as a rule, the most resistant hybrids fall in the tall-late subgroup, the least resistant in the short-early subgroup, and the rest in the two intermediate groups.

TABLE 2.—*Influence of height and lateness on the resistance to bacterial wilt in sweet-corn hybrids produced by crossing inbred strain M with various other inbred strains of the Golden Bantam type, and tested in 1934* [1] [2]

TALL HYBRIDS

Plot no. of hybrid	Index of resistance of other inbred	Maximum height of hybrid	Date of harvesting for canning	Index of resistance of hybrid	Plot no. of hybrid	Index of resistance of other inbred	Maximum height of hybrid	Date of harvesting for canning	Index of resistance of hybrid
		Inches					*Inches*		
19	25	63	Aug. 23	37	137	25	58	Aug. 25	25
49	0	56	Aug. 24	25	182	65	60	Sept. 1	56
71	19	57	Aug. 29	56	187	36	56	Aug. 23	25
74	25	56	...do...	41	189	36	55	Aug. 24	19
111	37	57	...do...	57	412	10	62	Aug. 21	25
134	72	66	Sept. 1	75					
135	56	62	...do...	75	Average...	34	59	Aug. 27	43

SHORT HYBRIDS

66	25	53	Sept. 1	65	190	45	47	Aug. 22	25
86	36	51	Aug. 27	35	191	42	53	Aug. 24	30
99	56	52	Aug. 29	56	192	34	52	...do...	30
145	52	45	Aug. 25	63	194	34	50	Aug. 25	30
150	32	54	...do...	49	195	0	51	Sept. 1	30
174	25	51	Aug. 29	35	196	29	51	Aug. 29	42
176	62	54	Aug. 25	50	197	41	50	Aug. 22	10
179	43	51	Aug. 27	62	199	41	52	Aug. 24	25
180	75	46	Aug. 29	59	201	15	48	Sept. 4	45
181	72	53	Aug. 24	56	202	42	51	Aug. 21	35
184	25	54	...do...	10	365	31	51	Aug. 22	25
185	29	47	Aug. 22	10					
186	10	45	Aug. 24	10	Average...	37	50	Aug. 26	37

EARLY HYBRIDS

19	25	63	Aug. 23	37	191	42	53	Aug. 24	30
49	0	56	Aug. 24	25	192	34	52	...do...	30
181	72	53	...do...	56	197	41	50	Aug. 22	10
184	25	54	...do...	10	199	41	52	Aug. 24	25
185	29	45	Aug. 22	10	202	42	51	...do...	35
186	10	45	Aug. 24	10	365	31	51	Aug. 22	25
187	36	56	Aug. 23	25	412	10	62	Aug. 21	25
189	36	55	Aug. 24	19					
190	45	45	Aug. 22	25	Average...	32	53	Aug. 23	25

LATE HYBRIDS

66	25	53	Sept. 1	65	174	25	51	Aug. 29	35
71	19	57	Aug. 29	56	176	62	54	Aug. 25	50
74	25	56	...do...	41	179	43	51	Aug. 27	62
86	36	51	Aug. 27	35	180	75	46	Aug. 29	59
99	56	52	Aug. 29	56	182	65	60	Sept. 1	56
111	37	57	...do...	57	194	34	50	Aug. 25	30
134	72	66	Sept. 1	75	195	0	51	Sept. 1	30
135	56	62	...do...	75	196	29	51	Aug. 29	42
137	25	58	Aug. 25	25	201	15	48	Sept. 4	45
145	52	45	...do...	63					
150	32	54	...do...	49	Average...	39	54	Aug. 29	50

[1] The average value for height of these hybrids was used to divide them into tall and short. Likewise the average harvesting date for canning was used to divide them into early and late. The differences in resistance among the various classes would have been considerably greater if only the extreme cases for height and lateness had been considered.

[2] The average index of resistance of inbred strain M was 36, and its average maximum height was 51 inches.

TABLE 3.—*Influence of the resistance in parent inbreds on the resistance of hybrids when strain M was crossed with various other inbreds of the Golden Bantam type* [1]

GROUP 1. HYBRIDS PRODUCED BY CROSSING INBRED M WITH OTHER INBREDS WITH AN INDEX OF RESISTANCE OF 0 TO 25

Plot no. of hybrid	Index of resistance of other inbred	Maximum height of hybrid	Date of harvesting for canning	Index of resistance of hybrid	Plot no. of hybrid	Index of resistance of other inbred	Maximum height of hybrid	Date of harvesting for canning	Index of resistance of hybrid
		Inches					*Inches*		
19	25	63	Aug. 23	37	184	25	54	Aug. 24	10
49	0	56	Aug. 24	25	186	10	45	...do	10
66	25	53	Sept. 1	65	195	0	51	Sept. 1	30
71	19	57	Aug. 29	56	201	15	48	Sept. 4	45
74	25	56	...do	41	412	10	62	Aug. 21	25
137	25	58	Aug. 25	25					
174	25	51	Aug. 29	35	Average	17	55	Aug. 28	34

GROUP 2. HYBRIDS PRODUCED BY CROSSING INBRED M WITH OTHER INBREDS WITH AN INDEX OF RESISTANCE OF 26 TO 50

86	36	51	Aug. 27	35	192	34	52	Aug. 24	30
111	37	57	Aug. 29	57	194	34	50	Aug. 25	30
150	32	54	Aug. 25	49	196	29	51	Aug. 29	42
179	43	51	Aug. 27	62	197	41	50	Aug. 22	10
185	29	47	Aug. 22	10	199	41	52	Aug. 24	25
187	36	56	Aug. 23	25	202	42	51	...do	35
189	36	55	Aug. 24	19	365	31	54	Aug. 22	25
190	45	47	Aug. 22	25					
191	42	53	Aug. 24	30	Average	37	52	Aug. 25	32

GROUP 3. HYBRIDS PRODUCED BY CROSSING INBRED M WITH OTHER INBREDS WITH AN INDEX OF RESISTANCE OF ABOVE 50

99	55	52	Aug. 29	56	180	75	46	Aug. 29	59
134	72	66	Sept. 1	75	181	72	53	Aug. 24	56
135	56	62	...do	75	182	65	60	Sept. 1	56
145	52	45	Aug. 25	63					
176	62	54	...do	50	Average	64	55	Aug. 29	61

[1] See footnote 2, table 2.

TABLE 4.—*Influence of height and lateness on resistance to bacterial wilt in hybrids from parent M crossed with inbreds having low (0 to 25), intermediate (26 to 50), and high (more than 50), indices of resistance* [1]

LOW—0 TO 25

Kind of hybrid	Plot no. of hybrid	Index of resistance of other inbred	Maximum height of hybrid	Date of harvesting for canning	Index of resistance of hybrid
			Inches		
Tall-late	71	19	57	Aug. 29	56
	74	25	56	...do	41
Average		22	57	...do	48
Short-late	66	25	53	Sept. 1	65
	174	25	51	Aug. 29	35
	195	0	51	Sept. 1	30
	201	15	48	Sept. 4	45
Average		16	51	Sept. 1	43
Tall-early	19	25	51	Aug. 23	37
	49	0	56	Aug. 24	25
	137	25	58	Aug. 25	25
	412	10	62	Aug. 21	25
Average		15	57	Aug. 23	28
Short-early	184	25	54	Aug. 24	10
	186	10	45	...do	10
Average		18	50	...do	10

[1] See footnotes 1 and 2, table 2.

TABLE 4.—*Influence of height and loteners on resistance to bacterial wilt in hybrids from parent M crossed with inbreds having low (0 to 25), intermediate (26 to 50), and high (more than 50), indices of risistance*—Continued

INTERMEDIATE—26 TO 50

Kind of hybrid	Plot no. of hybrid	Index of resistance of other inbred	Maximum height of hybrid	Date of harvesting for canning	Index of resistance of hybrid
			Inches		
Tall-late	111	37	57	Aug. 29	57
Short-late	86	36	51	Aug. 27	35
	179	43	51	...do...	62
	196	29	51	Aug. 29	42
Average		36	51	Aug. 28	46
Tall-early	150	32	54	Aug. 25	40
	187	36	56	Aug. 23	25
	189	36	55	Aug. 24	19
	191	42	53	...do...	30
Average		37	55	...do...	30
Short-early	185	29	45	Aug. 22	10
	190	45	45	...do...	25
	192	34	52	Aug. 24	30
	194	34	50	Aug. 25	30
	197	41	50	Aug. 22	10
	199	41	52	Aug. 24	25
	202	42	51	...do...	35
	365	31	51	Aug. 22	25
Average		37	49	Aug. 23	23

HIGH—MORE THAN 50

Tall-late	134	72	66	Sept. 1	75
	135	56	62	...do...	75
	182	65	60	...do...	56
Average		64	63	...do...	68
Short-late	(1)				
Tall-early	(1)				
Short-early	99	56	52	Aug. 29	56
	145	52	45	Aug. 25	63
	176	62	54	...do...	50
	180	75	46	Aug. 29	59
	181	72	53	Aug. 24	56
Average		63	50	Aug. 26	56

[1] None.

A similar type of analysis was applied to all of the F_1 hybrids tested in 1934 for which complete data were available and which could thus be classified. The results are summarized in table 5, where the hybrids are first divided into four classes on the basis of height and lateness, as tall late, tall early, short late, and short early. Further, each of the four classes of hybrids is divided into three groups, on the basis of the degree of resistance of the inbred parents composing the hybrids. The average measurements of height, harvesting date, and index of resistance for each group of hybrids is given for the purpose of making exact comparisons in determining the effect of a single factor on resistance. An examination of this table shows as a rule (1) that the taller and the later the hybrids are, the more resistant they are, and (2) that when the factors of height and lateness are about equal, hybrids produced from high-resistant inbreds are more resistant than hybrids produced from low-resistant inbreds.

TABLE 5.—*Influence of height and lateness of the hybrids upon hybrid resistance, and of parents' resistance upon hybrid resistance, in 229 hybrids tested for resistance to bacterial wilt in 1934* [1]

Kind of hybrid	Hybrids	Maximum height of hybrid	Date of harvesting for canning	Average index of resistance
	Number	*Inches*		
Tall late: [1]				
A, inbreds with index of resistance of 0 to 25	5	58	Aug. 29	28
B, index of resistance of one inbred 0 to 50 and the other 26 to 50	15	58	do	49
C, inbreds one or both of which had index of resistance higher than 50	19	61	Aug. 30	62
Total or average	39	60	Aug. 29	53
Short late:				
A, inbreds with index of resistance of 0 to 25	3	49	Aug. 30	13
B, index of resistance of one inbred 0 to 50 and the other 26 to 50	30	51	do	40
C, inbreds one or both of which had index of resistance higher than 50	17	49	Aug. 29	55
Total or average	50	50	Aug. 30	43
Tall early:				
A, inbreds with index of resistance of 0 to 25	31	60	Aug. 22	28
B, index of resistance of one inbred 0 to 50 and the other 26 to 50	26	60	Aug. 23	31
C, inbreds one or both of which had index of resistance higher than 50	12	60	Aug. 25	42
Total or average	69	60	Aug. 23	31
Short early:				
A, inbreds with index of resistance of 0 to 25	16	51	Aug. 22	17
B, index of resistance of one inbred 0 to 50 and the other 26 to 50	44	49	Aug. 23	30
C, inbreds one or both of which had index of resistance higher than 50	11	52	Aug. 25	44
Total or average	71	50	Aug. 23	29

[1] See footnote 1, table 2.

The data obtained for the group of 36 hybrids previously mentioned were further analyzed by the use of correlation coefficients. Simple and partial correlations for the various plant characters are presented in table 6. It appears that for this group of hybrids there is a positive correlation between resistance of the hybrids and (1) maturity of the hybrids, (2) resistance of the more resistant of the two parents, and (3) height of the hybrids, the significance of these correlations being in the order named. It is very likely that the value and significance of the correlation coefficients may change with the different hybrid groups under investigation. The multiple correlation coefficient for this group of hybrids is $R=0.866$ (or $R^2=0.735$), which indicates that approximately 73 percent of the resistance of the average hybrid of this group is correlated with the three hybrid characters mentioned above.

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TABLE 6.—*Simple and partial correlation coefficients among the various characters of a group of 36 F_1 hybrids* [1]

Simple correlations		Partial correlations	
Variables correlated [2]	*r* (coefficient of correlation)	Variables correlated	*r* (coefficient of correlation)
RhRp	[3] 0.600	*RhRp:HhMh*	[3] 0.634
RhHh	.297	*RhHh:RpMh*	.314
RhMh	[3] .720	*RhMh:RpHh*	[3] .737
RpMh	.254	*RpMh:RhHh*	−.169
RpHh	.084	*RpHh:RhMh*	[4] −.339
HhMh	.140	*HhMh·RhRp*	−.160

[1] A group of hybrids having a common parent, listed in tables 2 and 3.
[2] *Rp*=index of resistance of the more resistant of the 2 parents; *Rh*=index of resistance of the hybrids; *Hh*=height of hybrids; *Mh*=maturity (harvesting date) of hybrids.
[3] *P* value (level of significance) exceeds 1 percent point.
[4] *P* value (level of significance) exceeds 5-percent point.

DOMINANCE RELATIONSHIPS OF RESISTANCE

INSTANCES OF RESISTANCE DOMINANCE

Evidence that the resistance of the parent inbreds is transmitted to the F_1 hybrids in most cases as a dominant is further considered through studies both on groups of hybrids and on individual hybrids. One instance has already been mentioned in connection with table 3 where the average index of resistance of each of the three groups of hybrids appeared to follow closely that of the more resistant parent. More examples of dominance of resistance in groups of hybrids are presented later. In examining the various hybrids for the dominance relationships, one should consider at the outset (1) the height and lateness of each parent and the varying effect of these parent characters upon the height and lateness of the hybrids, and (2) the effect of height and lateness of the hybrids upon the resistance of the hybrids. The interplay of these commonly interrelated characters within a certain individual hybrid, together with the different extent of heterosis exhibited by different hybrids, may often obliterate the expression of resistance dominance, while in another individual hybrid they may create a false appearance of dominance. It seems that because of the interaction of the various resistance factors and because of some exceptions, evidence obtained as a result of analysis based on relatively large hybrid groups as a whole may be more valuable in demonstrating the general principles of resistance than evidence based on the examination of only one or a few hybrids. However, this second approach is not to be ignored, and a study of dominance of resistance has been made in some inbreds and hybrids selected for the purpose.

Thus, individual hybrids in which resistance appeared dominant are shown in table 7. These are the only hybrids among all those tested in 1934 which could be analyzed for resistance dominance without the confusing influence of the characters of height and lateness of both parents and hybrids. Thus, in the case of hybrid 182, both parents are of the same class, namely, tall-late, and produced a hybrid also of the

same class. Both parents had the same silking date, were approximately of the same height, and produced a hybrid with the same silking date and of approximately the same height. The only difference between the two parents was in the degree of resistance, one having an index of resistance of 36 and the other of 65. The hybrid had an index of resistance of 56, a figure closer to that of the resistant parent than to that of the susceptible, thus indicating the dominant character of resistance. The next two hybrids (95 and 265) in table 7 show resistance dominance even more clearly. Hybrids 22, 24, and 25 are short-early, all very susceptible (the last two are reciprocal), and were made from short-early susceptible inbreds. Among the group of hybrids produced from short-early, low-resistant inbreds, there were some which showed an appreciable degree of resistance. These same hybrids, however, were relatively tall and could not be classed as short-early. The resistance of these hybrids was correlated with the increased height resulting from the hybridization.

TABLE 7.—*Dominance of resistance to bacterial wilt shown in selected individual hybrids and their parents in which the confusing influence of height and lateness have been eliminated*

Plot of hybrid	Type of inbreds from which the hybrids were made	Index of resistance of—	
		Inbreds	Hybrids
182	Tall-late, high index of resistance	65	56
	Tall-late, low index of resistance	36	
95	Short-late, high index of resistance	56	55
	Short-late, low index of resistance	25	
265	Short-early, high index of resistance	62	61
	Short-early, low index of resistance	30	
22	Short-early, low index of resistance	0	0
	do	0	
24	Short-early, low index of resistance	0	0
	do	0	
25	Short-early, low index of resistance	0	0
	do	0	

CUMULATIVE EFFECT OF PARENTS' RESISTANCE IN RELATION TO DOMINANCE

The question whether the resistance of the hybrids is influenced only by the more resistant of the two parents or by the combined resistance of the two parents was given further consideration. The data on a randomized group of 44 unrelated hybrids tested in 1935 is shown in table 8. Each of these hybrids was made by crossing two different inbred parents, one highly resistant, having an index of resistance of approximately 70, and the other having an index of resistance varying from 0 to 69. These hybrids were divided arbitrarily into four groups according to the resistance of the less resistant of the two parents. Table 8 shows no great differences in resistance among the four groups of hybrids, and it would seem that the resistance of the hybrids was mainly determined by the more resistant of the two parents. Thus the resistance of the parents, with the possible exception noted in the following paragraph, does not have an apparent significant cumulative effect in most hybrid combinations.

TABLE 8.—*Influence of the two parents having different degrees of resistance upon the resistance of the hybrids to bacterial wilt; 1935 trials*

Groups of hybrids, the more resistant parent of which had an index of resistance of approximately 70, and the less resistant parent, an index of resistance varying from 0 to 69	Hybrids	Maximum height of hybrids and parents	Average silking date of hybrids and parents	Average index of resistance of hybrids and parents
1, index of resistance of less resistant parent from 0 to 20:	*Number*	*Inches*		
Hybrid	8	78	Aug. 3	69
More resistant parent		66	Aug. 5	70
Less resistant parent		63	July 31	14
2, index of resistance of less resistant parent from 21 to 40:				
Hybrid	16	75	Aug. 6	65
More resistant parent		64	do	69
Less resistant parent		58	Aug. 5	34
3, index of resistance of less resistant parent from 41 to 60:				
Hybrid	14	77	Aug. 6	64
More resistant parent		68	do	68
Less resistant parent		59	Aug. 5	49
4, index of resistance of less resistant parent from 61 to 69:				
Hybrid	6	79	Aug. 5	66
More resistant parent		64	Aug. 6	69
Less resistant parent		70	Aug. 4	68

DEGREES OF PARENTS' RESISTANCE IN RELATION TO DOMINANCE

In the results of 1934 there were some indications that when a hybrid was made of inbreds one or both of which had a relatively high resistance, the resistance of the hybrid was usually about as high as that of the more resistant parent. On the other hand, when a hybrid was made of inbreds both of which had a relatively low resistance, the resistance of the hybrid was usually higher than that of either parent. These occurrences were particularly apparent in the trials of 1935, the results of which are presented in table 9. Thus in the class of tall-late hybrids for instance, in group A, the indices of resistance for the two parents are 39 and 24, and that for the hybrid is 50. The index of resistance of the hybrid exceeds that of the more resistant parent by 11 points. On the other hand, in group B, the indices of resistance for the two parents are 68 and 46, while that for the hybrid is 65, a value closely approximating that of the more resistant parent. Similar relationships are found in the other three classes of hybrids in table 9. So far the explanation of these relationships is not clear. However, a working hypothesis partly concerned with hybrid vigor is offered under Discussion.

IMPORTANT EXCEPTIONS TO GENERAL RULES REGARDING HYBRID RESISTANCE

Some exceptions to the already stated general rules on hybrid resistance have been found in almost all experiments. Some of these exceptions may have been due to variations in the material or environment, others to errors in technique, while still others, and particularly some of the more striking ones, may be inherent in the problem. For instance, there were a few hybrids which showed a low degree of resistance in spite of the fact that one of the parent strains had a high index of resistance. Some other hybrids showed resistance intermediate in degree between that of the parents. Such exceptional cases would require special study and interpretation. These cases

seem to suggest that the mode of transmission of the resistance qualities may be of more than one type and that it may depend upon the material employed.

TABLE 9.—*Influence of parents' resistance upon resistance of hybrids to bacterial wilt in cases of hybrids produced from low-resistant and high-resistant parents; 1935 trials*

Kind of hybrid[1]	Hybrids	Maximum height of hybrids and parents	Average silking date of hybrids and parents	Index of resistance of hybrids and parents
	Number	*Inches*		
Tall-late:	29			
A, index of resistance of neither parent exceeding 50:				
Hybrid	13	77	Aug. 7	50
More resistant parent		62	Aug. 6	39
Less resistant parent		57	Aug. 5	24
B, index of resistance of one or both parents exceeding 50:				
Hybrid	16	82	Aug. 7	65
More resistant parent		64	do	68
Less resistant parent		61	Aug. 6	46
Average:				
Hybrid		80	Aug. 7	58
More resistant parent		64	Aug. 6	55
Less resistant parent		59	Aug. 5	39
Short-late:	31			
A, index of resistance of neither parent exceeding 50:				
Hybrid	20	69	Aug. 8	56
More resistant parent		62	Aug. 6	36
Less resistant parent		57	Aug. 5	28
B, Index of resistance of one or both parents exceeding 50:				
Hybrid	11	67	Aug. 7	63
More resistant parent		60	Aug. 5	66
Less resistant parent		61	do	41
Average:				
Hybrid		68	Aug. 8	59
More resistant parent		61	Aug. 5	47
Less resistant parent		59	do	33
Tall-early:	40			
A, index of resistance of neither parent exceeding 50:				
Hybrid	13	77	Aug. 3	60
More resistant parent		60	Aug. 6	40
Less resistant parent		56	Aug. 5	29
B, index of resistance of one or both parents exceeding 50:				
Hybrid	27	77	Aug. 3	66
More resistant parent		63	Aug. 4	67
Less resistant parent		57	Aug. 3	37
Average:				
Hybrid		77	do	64
More resistant parent		62	Aug. 4	58
Less resistant parent		56	Aug. 3	32
Short-early:	50			
A, index of resistance of neither parent exceeding 50:				
Hybrid	26	69	do	50
More resistant parent		60	Aug. 4	42
Less resistant parent		58	Aug. 3	25
B, index of resistance of one or both parents exceeding 50:				
Hybrid	24	70	Aug. 2	67
More resistant parent		60	do	66
Less resistant parent		59	Aug. 3	40
Average:				
Hybrid		69	Aug. 2	58
More resistant parent		60	Aug. 3	54
Less resistant parent		59	do	32

[1] See footnote 1, table 2.

Some early resistant hybrids have been obtained by taking advantage of the fact that in crossing two inbreds, the resulting hybrid in some cases was earlier than either of the two parents. Such differ-

ences in maturity between inbred parents and hybrids ordinarily varied from 1 to a few days, and in a few exceptional cases, to 2 weeks.[11] These relatively earlier hybrids in most cases did not show a lower degree of resistance than either of their later maturing parents. However, in the very few exceptional cases where the difference in maturity between parents and hybrids was relatively great, from 10 to 14 days, the hybrids did show an appreciably lower degree of resistance than that of either parent.

Early resistant hybrids were also produced by crossing an early resistant inbred possessing "true resistance", with another inbred of the same type, or with another early inbred regardless of its degree of resistance. These hybrids have so far withstood the severest inoculations without appreciable reduction in yield at the time of harvesting for canning. Like all the rest of the hybrids and inbreds inoculated, they showed the characteristic leaf stripes, but appeared to recover from the disease as growth progressed.

DISCUSSION

In order to clarify some of the more pertinent concepts in this paper, a brief discussion follows of (1) the resistance of the inbred lines, (2) the height and lateness of the hybrids in regard to resistance, and (3) the inheritance of resistance.

The inbred lines may for convenience be classified in four categories on the basis of resistance: (1) Those with resistance correlated mainly with height, (2) those with resistance associated chiefly with lateness, (3) highly resistant lines with resistance not correlated with either of these characters, and (4) those with a very low degree of resistance, even though they are relatively tall and late. The last two categories of inbreds are very rare, probably comprising less than 0.5 percent of all the inbreds tested. The majority of the inbred lines, however, possess resistance which is associated with height and lateness of the plants. In most cases it would be difficult to determine to what exact degree the resistance of a particular inbred is associated with its height and lateness.

In the hybrids as in the inbreds, height and lateness seem to be associated with resistance. Relatively late hybrids as a rule showed greater resistance than relatively early hybrids. The data in tables 2 and 4 for a group of 36 hybrids with one common parent consistently show that the tall-late hybrids have a higher index of resistance than the short-early hybrids. The same association is even more strikingly brought out in the data for 229 hybrids, shown in table 5, where the tall-late hybrids have an index of resistance of 53 while the short-early hybrids have an index of 29, a difference of 24 points. The difference in height between these two groups was only 10 inches, and the difference in date of harvesting was only 6 days. Individual hybrids differing in height by about 2 feet and in silking date by more than 14 days showed differences in resistance of 80 or more points.

The correlation between height and lateness and hybrid resistance seems to diminish from year to year as the "true resistance" of the composing inbreds increases. Thus in 1933 the difference in resist-

[11] These differences in maturity between the inbreds and the hybrids seemed to vary to a certain degree with the season. In 1934 they were more common than during the other two seasons. In the majority of cases, however, the hybrids did not appreciably differ in maturity from the parent inbreds.

ance between the tall-late and short-early hybrids was considerable and the most resistant hybrids were found only among the tall-late class of hybrids. In 1934, because of the number of early, relatively resistant inbreds employed in their making, the hybrids showed less tendency to correlate resistance with height and lateness, as many of the early hybrids showed considerable resistance. Still, the hybrids tested in that year as a whole showed a definite correlation between height and lateness on the one hand, and resistance on the other, as may be seen in table 5. The hybrids tested in 1935 were derived mainly from relatively early-resistant inbreds and as a whole showed hardly any correlation between height, lateness, and resistance (table 9). Nevertheless, some of the most resistant hybrids even in that year were among the tall-late class, and some of the most susceptible ones, among the short-early class.

The inheritance of resistance from the inbreds to the hybrids seems evident from data presented in tables 3, 5, 7, 8, and particularly table 9. That the low-resistant inbreds (groups A of table 9) produced as a rule less resistant hybrids than the high-resistant inbreds (groups B) is apparent from the index of resistance of these hybrids in each of the four classes shown. These indices are 50 and 65, 56 and 63, 60 and 66, 50 and 67. In general, these results confirm those obtained in 1934 (table 5), although some exceptions have been noted.

The dominant character of resistance is evident in these results. In each group or class of hybrids shown in table 9, the index of resistance seems to approach that of the more resistant of the two parents, and in the case of the A groups it seems to exceed that of the more resistant parent. This increase in resistance of some hybrids, of those produced from low-resistant inbreds, over the resistance of the inbred parents may be attributable to the additive effect of a great number of resistance factors. From the evidence available, however, it seems more likely that it is associated with the increased height resulting from hybridization, as has already been observed in the case of the 1933 and 1934 hybrids as a whole.

An explanation as to why hybrid vigor may be associated with considerably increased resistance in the case of hybrids produced from low-resistant inbreds, and may not be so associated in the case of hybrids produced from high-resistant inbreds, seems desirable. To obtain a satisfactory explanation would require the performance of additional special tests. As a working hypothesis, however, it may be assumed (1) that each of the three types of resistance, height-correlated, lateness-correlated, and "true resistance", within a hybrid has a certain value, and (2) that the resistance of the average hybrid is not ordinarily expressed by the sum total of the values of the three resistance types but rather by the highest one of the three values; i. e., the three types of resistance have only a minor, if any, additive effect, and the highest prevails over the other two. If such an assumption is correct, then, in the case of average hybrids produced from low-resistant inbreds, the height-correlated resistance of the hybrids might exceed the resistance value of the inbreds. Thus, the hybrid would have an index of resistance higher than that of either of the two parent strains. However, in the case of hybrids produced from high-resistant inbreds (in many cases the inbred's resistance may be largely of the "true resistance" type), the transmitted resistance of the parents might exceed the height-correlated resistance of

the hybrids. In such cases the index of resistance of the hybrids would be approximately equal to that of the more resistant parent strain.

The data have shown that as a whole when hybrids are made from highly resistant inbred strains, the resistance of these hybrids is governed primarily by the resistance of the inbreds. In such cases the height and the lateness of the resulting hybrids seem to play a secondary role. It is from such early resistant inbred lines, obtainable by careful searching, inbreeding, selecting, and continuous testing by artificial inoculation, that tall and vigorous, early resistant hybrids may be produced to serve the needs of the canners and market gardeners.

SUMMARY

Studies on resistance of inbred strains and crosses of sweet corn to bacterial wilt of maize caused by *Phytomonas stewarti* were made during the growing seasons of 1933, 1934, and 1935. The sweet corn tested for resistance included approximately 1,000 inbred strains and 1,000 F_1 hybrids and top crosses of the Golden Bantam type. The plants were tested by artificial puncture inoculation and by natural infection, when that occurred. Preliminary trials were made to determine comparative efficiency of various methods of inoculation, period of greatest host susceptibility, age of host plant in relation to type of symptom expression, comparative rate of wilting of hybrids and their respective inbred parents, time for final record taking, uniformity of inoculation, and comparative value of artificial puncture inoculation and natural infection. Artificial inoculation was found to have certain important advantages over natural infection as a method of testing for resistance. The results obtained are as follows:

Great differences in resistance were found among the inbred strains. As a rule, the taller strains showed greater resistance than the shorter strains, and the later strains showed greater resistance than the earlier strains. A few relatively short-early strains showed a high degree of resistance, and a few tall-late strains showed a low degree of resistance.

The hybrids and the top crosses, like the inbreds, showed wide variations in resistance. The resistance of the hybrids was found to be inherited from the inbred parents. Resistant inbreds in most cases produced resistant hybrids, and susceptible inbreds produced susceptible hybrids.

Resistance in the hybrids appeared to be generally dominant. As a rule, crosses between resistant and susceptible inbreds gave resistant hybrids, crosses between resistant inbreds and resistant inbreds gave resistant hybrids, and crosses between susceptible inbreds and susceptible inbreds gave susceptible hybrids.

Tall and late hybrids were found to be, as a rule, more resistant than short and early hybrids.

Hybrids produced from highly resistant inbreds generally showed high resistance regardless of their degree of earliness or lateness. Highly resistant hybrids were commonly late although a few were early.

Hybrid height usually indicating hybrid vigor as a rule increased resistance, particularly in the case of hybrids produced from relatively low-resistance inbreds.

The top crosses reacted like the true hybrids in all respects.

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